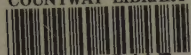


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Acta Psych. et Neurol. Suppl. 59/1950

Acta Path. et Microbiol. Scand. Suppl.

17 1933

Zeit. f. d. ges. exp. med. 59 1928

Montreal M.J. 24 1895-96

Brit. Heart J. 3 1941

Anat. Record 19 1920

Acta Orthop. Scand. 17 1947-48

Beit. z. Chem. Physiol. u. Path. 4

Biol. Symp. 10

Biochem. Zeit. 144 1924

THE ANATOMICAL RECORD

19032

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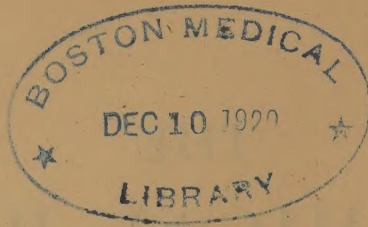
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VOLUME 19

JUNE—NOVEMBER, 1920

PHILADELPHIA
THE WISTAR INSTITUTE OF ANATOMY AND BIOLOGY



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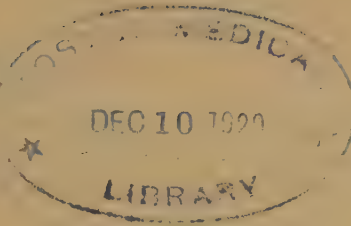
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Resumen por el autor, John Shelton Horsley, Jr.,
Universidad de Virginia.

Descripción de un perro con seis patas.

El presente trabajo es una descripción detallada de la anatomía externa e interna de una perra joven que poseía un par adicional de patas posteriores bastante normales y colocadas simétricamente. Este monstruo presentaba un par de pelvis casi normales fusionadas entre sí, una cloaca en el lado derecho, ano y vagina separados en el lado izquierdo, dos vejigas urinarias, un solo riñón, un uréter impar en conexión con la vejiga izquierda, un solo intestino delgado, dos colon, dos ciegos con sus correspondientes apéndices, glándulas suprarrenales pares y dos úteros provistos cada uno de un tubo uterino y un ovario. Las tibias de las patas supernumerarias estaban fusionadas.

Translation by José F. Nonidez
Cornell University Medical College, N. Y.



A DESCRIPTION OF A SIX-LEGGED DOG

JOHN SHELTON HORSLEY, JR.

Department of Anatomy, University of Virginia

SIXTEEN FIGURES

On January 11, 1919, Mr. John R. Raines, a farmer living near the University, brought to Prof. H. E. Jordan's laboratory a dead female dog with an extra pair of hind legs. The thoracic and abdominal cavities were opened and the dog at once placed in a 10 per cent solution of formalin. This specimen was subsequently turned over to me for study and description. The work was done in the Laboratory of Histology and Embryology under the supervision of Professor Jordan, to whom I am greatly indebted for the privilege.

From Mr. Raines were secured the following data: The dog was born October 7, 1918; died from exposure to cold the night of January 9, 1919. Her father was a shepherd, her mother a bull-terrier; both parents were apparently normal. The litter included in addition to this abnormal individual one normal brother and three normal sisters. The six-legged puppy appeared in life otherwise normal and healthy, and was apparently but little inconvenienced in walking and running by the extra pair of legs, which she carried slightly raised above the ground. The unpaired tail was apparently under perfect control.

EXTERNAL APPEARANCE

As regards the shape and general appearance of the head this dog more nearly resembled a fox-terrier, and she was about the size of this type of dog (fig. 1). With the exception of the nipples, she appeared normal cephalad of the umbilicus. With the exception of the tail and anus, she was double caudad of this point.

Closer examination revealed the following details: The leg, vagina, anus, and tail of the left side were displaced about 1 cm. laterad of their normal relative position with respect to the vertebral column. The sagittal plane of the proximal portion of the tail made an angle of 25 degrees with that of the vertebral column. The right leg was displaced slightly forward and dextrad of its normal position. It was slightly smaller than the left leg and presented a rather undeveloped appearance, especially in the size of the thigh muscles. Between these two legs hung the extra pair of legs. The pair was inclined a little to the right of the medial line and it was enveloped in a common integument as far distally as the ankles. The members of the pair were of approximately equal size and represented genuine hind legs. Barring a very slight ventral bend at the level of the knees, the pair was extended in a straight line and it was placed in such a way that the pads of the feet faced toward the ground when the dog was standing. The pair measured 18.5 cm. from the heads of the femurs to the tips of the toes. These extra legs were only slightly more slender and shorter than the other two hind legs. Palpation indicated a fusion of the tibiae, a conclusion confirmed by roentgenograms (figs. 2 and 3) and subsequent dissection. The extra legs articulated with the medial surfaces of the opposite halves of the paired pelvises slightly forward, and to the right, of the root of the tail. There was no second tail or anus, but there was a second set of external genitalia 2 cm. below and to the right of the articulations of the extra pair of legs. The vertebral column in the region of the sacrum seemed abnormally wide on the right side and presented abnormal landmarks, description of which will be reverted to subsequently. Just below the right side of the double knee there was a roughened scar-like area, whose significance will also be indicated below.

INTERNAL ANATOMY

Osteology

The vertebral column contained the usual number of vertebrae, namely seven cervical, thirteen thoracic, seven lumbar, three sacral, and nineteen caudal (fig. 2). It remained single throughout and was normal as far as the seventh lumbar vertebra, which latter was normal on the left side, but presented a large well-rounded mammillary process that was twisted dorsally and slightly caudally extending on the same level with that of the corresponding vertebral spine. The sacrum was very slightly bent to the left. On the right the articular surface of the first sacral vertebra was turned dorsally, and accordingly produced a slight elevation. There was also on the right side an oblong, irregular plate of bone that measured 10 mm. in length, 7 mm. in thickness, and 6 mm. in the vertical plane (fig. 4, *M*). It was fused with the first and second sacral vertebrae, and represented a second deformed sacrum. On the left side the sacropelvic articulation was normal with the exception of a small piece of bone, 8 mm. in length, which jutted out caudally from the left ilium at the level of the sacrum and was fused with the second and third sacral vertebrae. There was a gentle curve to the left, formed by the first three caudal vertebrae, the first of which articulated on its right side with the base of the fused ilia. The remaining caudal vertebrae were normal.

Two pelves were present (fig. 3). At first observation there seemed to be a smaller medial pelvis fused dorsally to a larger and practically normal ventral pelvis; but after closer examination of all of the related structures the conclusion was reached that the condition was one of lateral fusion between a right and left pelvis. The course of the unpaired sciatic nerve is the only obstacle to the latter interpretation. The right and left lateral ilia were of normal size (figs. 4 and 5). The left ilium articulated with the sacrum of the left side in the usual manner, with the exception of the intervention of a small spur of bone extending caudally from it. This has already been described. The crest of the right ilium was displaced cephalically 1 cm. and dorsally

3 mm. A small triangular piece of bone, 1.5 cm. in length, articulated with the right deformed sacrum by a number of strong ligaments forming an amphiarthrosis (fig. 4 *N*). The crests of these lateral ilia were about 6 mm. further apart than they should have been if the right had its normal position and the two considered part of one pelvis.

The right and left medial ilia were fused to form one bone which presented a dorsally protruding crest (fig. 4). This fused medial ilium was approximately a third the size of the normal lateral ilia. The vestigial right sacrum was fused with the base of the medial fused ilium. These two structures were continuous on the ventral surface, but dorsally there was a depression partially separating them. On the left the base of the fused ilium was joined to the third sacral vertebra by a synchondrosis, and with the first (proximal) caudal vertebra by a syndesmosis. This fusion of the ilia had brought the two medial acetabula so close together on the dorsal surface that they nearly touched each other (fig. 5). The long axis of this medially fused ilial portion of the compound pelvis made a 15 degree angle with the midline on the right side. If considered as a dorsally interpolated pelvis, it would be about half the size of the larger pelvis.

The two medial ischia formed a basin, which was open dorso-caudally and closed ventrocephalically, presenting on each side the relatively high crests of the two medial tubera ischii. The basin measured 3.7 cm. from crest to crest (fig. 5). In this basin lay the necks and proximal fourths of the femurs of the extra two legs, along with that portion of the heads that did not enter directly into the hip-joints (fig. 4). The two obturator foramina opened ventrocephalically through each side. They were completely closed by thin ligamentous bands and were of about half the normal size. Caudal to the fusion of the medial ilia, and also to the acetabula, there was a very firm union between the right and left pelvises along the whole length of the pubo-ischial symphysis of each (fig. 5). This line of fusion would call for the same description whether the fused pelvises were interpreted as right and left or dorsal and ventral components.

The heads of the femurs of the extra two legs were about 1 mm. apart and articulated with the two medial acetabula, each forming an enarthrosis. The articulations were alike on both sides, and normal to the extent that they formed ball-and-socket joints, with synovial bursae, ligamentous capsules, etc. There was a slight twisting, however, produced by their abnormal positions. All of the structures that entered into these articulations were of approximately half the size of the corresponding structures of the normal right and left lateral hip-joint. The movements of these articulations were limited practically to a dorsoventral action due to the fusion of the tibiae of the two extra legs (fig. 3).

The right and left lateral ischia were of normal size, but were slightly twisted laterally, the right more so than the left. The crest of the right lateral tuber ischii was 1 cm. laterad of that of the right medial tuber ischii at the widest point (fig. 4). The right colon, vagina, and urethra united within the basin formed by these ischia into a cloaca (fig. 12). The opening of this basin was the pelvic mouth of the right pelvis. The corresponding crests of the left side were 2 cm. apart at their widest points and formed a somewhat less constricted basin for the left vagina. The aperture of this basin was the pelvic mouth of the left pelvis (fig. 5).

The bones of the right and left lateral legs were normal. Those of the extra two medial legs were very slightly shorter and slightly more slender than the lateral ones, as may be seen in figure 3. The tibiae of the supernumerary legs were fused medially along their whole extent. The fibulae appeared slightly larger than normal, the left fibula being more intimately fused with its tibia (fig. 3). No other marked abnormalities occurred in the bony structures. The double knee-joint was practically immobile except for a very slight action in the caudocephalic direction.

Myology

The muscles of the left lateral leg, thigh, and hip regions were normal; those of the right thigh also appeared normal except for a somewhat smaller size.

In the hip region of the two extra legs there occurred only a very few small muscles that passed down to the thigh. These muscles were inserted along the proximal portions of the two femurs and seemed to represent only remnants. There was a layer of superficial fascia over the whole of this muscle mass. Some atrophic vestigial muscles covered the popliteal fossae extending up over the distal two-thirds of the two femurs and down well over the ventral portion of the knee-joint. They were better developed on the left member than on the right. The space between the two femurs was occupied by an artery, a vein, a large nerve, and an abundance of loose connective tissue. The two legs of the extra pair were bound together by a superficial layer of fascia and the integument. There were two very distinct tendons of Achilles; the one of the left leg was more pronounced, and it was stretched so tight as to permit only very little movement of the left foot. The right foot was more free to move. The flexor digitorum brevis tendons were very distinct on the feet, but none of the muscles could be found. No muscles occurred beyond the extreme proximal ends of the fused tibiae; there was an enveloping layer of superficial fascia along their entire length.

The ligamentum nuchae was the only abnormal structure observed cephalad of the diaphragm. This was a very thick, round ligament rather than, as usual, a thin ligamentous raphé.

Splanchnology

The stomach, small intestines, liver, gall-bladder, spleen, and pancreas were unpaired and apparently normal.

The large intestines were double; one colon was very much distended and lay ventrad and to the right of a smaller colon (figs. 6, 7, and 8). The former had very short ascending and transverse portions, but a long descending portion which was constricted in the middle. This constriction produced two large sacculations, the caudal being the more distended. The wall of this portion was rigid and brittle, apparently lacking muscle constituents. This larger colon passed through the right pelvic

mouth and opened into the vagina of the right side, thus contributing to the formation of a cloaca. The smaller colon of the left side had neither teniae nor sacculations; and there were practically no corresponding ascending or transverse portions. It joined a normal rectum which ended in a normal anus; it was on the whole more nearly normal than the right colon. Feces were found in both colons, and there were no adhesions or constrictions that could hinder either from functioning.

The ilioecolic portion of the small intestine was slightly enlarged, and at this point of enlargement the two colons anastomosed with each other and with the small intestine (fig. 6). Each colon had a caecum with an appendix. The right caecum was the larger and, excepting its increased size and its associated appendix, it seemed normal. This appendix was a constricted apical portion of about 1.5 cm. in length (fig. 6). The left caecum was very short, being about 1 cm. long. Its appendix had a smaller diameter than that of the right and was about three times as long (fig. 7). It was sharply folded at four distinct points into a compact structure.

The single ileocolic valve was relatively large and covered both colic orifices, but was thickened in that portion overlying the right orifice (fig. 8). Its opening was directed somewhat laterally and gave vent nearly directly into the left colon. At a point immediately distal to the valve the lumens of the two colons united. On account of the thickening of one side of the valve, the connection between the lumens of the right colon and the small intestine was thrown to the left, somewhat toward the smaller colon. The caecocolic orifices of both colons were apparently normal (fig. 8). It may be of interest to note that there were ten persimmon seeds and a few whole grains of corn in the right colon. The great enlargement of the right colon may find its explanation in a gradual distention by fecal contents which could be only slowly voided due to lack of peristalsis following the paucity or lack of smooth muscle.

On the right side the larger colon, the urethra, and the vagina had a common exit chamber, forming a cloaca (fig. 12). The right rectum formed the largest part of this chamber, and on

this account the orifices of the vagina and the urethra seemed to empty into it at a point about 3 cm. cephalad of the common external opening, the vagina on the medial and the urethra on the lateral sides, respectively.

The external genitalia of that side were slightly smaller than those of the left, but had a generally normal appearance.

The urogenital system

The single kidney was situated on the left side. No trace of even a vestigial kidney could be found on the opposite side. This lone kidney, located at the usual level, was considerably larger and more spheroidal than normal (fig. 9). It received a large renal vein from the left side of the inferior vena cava; and slightly dorsad and caudad of this point it received a renal artery from the abdominal aorta. Midway between the latter and the pelvis of the kidney the renal artery divided into two, one entering dorsally and the other, after curving around the renal vein, entering ventrally and cephalicly to it. Before entering the pelvis the renal vein gave off a branch that coursed laterally over the ventrocaudal portion of the kidney to the left ovary and oviduct. A single large ureter passed caudally to empty into the left urinary bladder in a normal way (fig. 10). The minute anatomy of this kidney was perfectly normal. Cephalad of the kidney, and in their proper positions, occurred two adrenals (fig. 9).

Of the two urinary bladders the left was apparently normal, except that it was slightly displaced to the left. The displacement was due chiefly to the presence of the greatly distended right colon. This bladder was completely collapsed. Its urethra was normal, emptying by means of the left vagina (fig. 10). The right urinary bladder was rigid and distended. It was composed of brittle tissue apparently like that of the larger colon. It was obviously smaller than the left bladder when the latter had become distended. At its cephalic end there was a narrow circular area (3 mm. in diameter) of very delicate tissue simulating a membrane, which yielded on the slightest pressure (fig.

11). There was no vestige of a ureter in connection with this bladder. Its urethra had about twice the normal diameter, and was composed of the same kind of brittle tissue as the bladder. A medial longitudinal section of the bladder revealed a lining of elastic tissue that was hard to peel off and that had the macroscopic appearance and general consistency of a thin plate of cartilage. Irregular partitions extended from the walls forming two large pockets at the cephalic and caudal ends of the bladder, respectively (fig. 11). Between these and in the central portion there were about ten smaller pockets. Along the entire ventral wall there was a space between this cartilage-like lining and the wall of the bladder which was continuous with the lumen of the urethra (fig. 11). The urethra had a very thick wall and emptied into the cloaca (fig. 12).

The genital organs

Two ovaries, each with its respective uterine tube (unpaired cornu uteri) leading to a respective uterus (corpus uteri), were situated in their normal positions. The ovary of the left side was flattened and oval in outline; that of the right side was flattened, elongated, and almost crescent-shaped, with a deep longitudinal groove extending over its lateroventral surface. The two uterine tubes extended caudomedially to their corresponding uteri (figs. 12 and 13). The right tube was the shorter and slightly the thicker of the two. The right uterus was about twice as long and thick as the left. The latter presented no peculiarities in its continuation into the vagina of the left side. The right vagina was relatively short; it was continued into the common chamber which formed the cloaca. Both uteri were abnormal to the extent that they were unicornuate.

Four rows of asymmetrically distributed nipples, twelve in number, were present (fig. 14).

Angiology

The blood supply of the kidney has been described above. No traces of any blood-vessels that might have corresponded to the right renal artery and vein could be found.

The abdominal aorta and the inferior vena cava remained single throughout their entire course, but they gave off extra branches which supplied the supernumerary structures. The distribution of these two chief vessels and their principal branches is shown in figure 15. The abdominal aorta gave off a right common iliac artery a short distance cephalad of its usual place of branching. The left common iliac was larger than the right and seemed to represent a direct continuation of the abdominal aorta. Its course was in direct line with that of the aorta to a point about 1 cm. caudad of the point of branching of the right common iliac. Here there was a gentle curve to the left, the main portion being continued as the left external iliac which proceeded down the left lateral leg as the femoral artery. Slightly caudal to the beginning of this curve on the left common iliac just mentioned, and on the outside of it, a large branch came off which supplied the two extra legs. Very close to the origin of this larger branch there was a small branch which went to the left urinary bladder; while just caudal to this a larger one came off and divided into two, the medial representing the caudal (middle sacral) and going to the tail, the lateral going to the structures in the left pelvic cavity and probably representing the left internal iliac artery.

One principal artery and one principal vein supplied the two extra legs. The plan of the arterial supply is represented in figure 16; that of the venous supply is practically identical. The vessels continued their course caudally between the two femurs, giving off two small branches, one on each side, just distal to the heads of the femurs, to supply the scanty muscles and fascia of that region. No other branches were discernible cephalad of a level about 2 cm. proximal to the knee-joint. At this point, however, both the artery and the vein divided into one medial and two lateral branches, the two lateral branches of

each vessel passing distally to the lateral sides of the fused tibiae and finally coming around on the dorsal side to form an anastomosing arch over the distal portion of the tibiae in the region of the ankle. From this arch sprang two main arteries and veins which passed on to supply the feet, the right set to the right foot and the left set to the left foot. Two medial smaller branches arose from the arch and supplied the structures in the immediate vicinity. The medial branch (fig. 16 *M*) of the principal vessels mentioned above represented a terminal branch. The medial artery and vein passed distally along the ventral line of fusion of the two tibiae where they became resolved into branches that supplied the structures of the ventral portion of the fused legs. The lateral branches supplied the structures of the lateral and dorsal surfaces. The venous system of the supernumerary legs paralleled the arterial system throughout its entire course.

Numerous lymph nodes were found scattered throughout the abdomen. Just cephalad of the kidney occurred the two largest nodes. The smaller nodes were relatively more abundant along the inferior vena cava and the abdominal aorta. Those of the paired pelvic cavities were rather large and numerous. A large bean-shaped lymph node, about 1 cm. in length, was situated at the level of the stifle-joint on the ventral side. This probably represented a composite popliteal node and was apparently the only lymph node of the two extra legs.

Neurology

A large nerve accompanied the principal artery and vein of the two extra legs. This nerve presented an oval cystic enlargement, macroscopically suggestive of a ganglion, at the point where it entered the double leg, just distal to the heads of the two femurs. The nerve passed dorsal to the blood-vessels, accompanying them as far as they went, and then accompanying the terminal or medial branch down over the midline of the double stifle-joint. As the nerve passed the latter point it presented a gradual cone-shaped enlargement and, turning laterally and dorsally around the medial condyle of the head of the

right tibia, ended abruptly in the skin (fig. 16). On the external surface of the skin this termination presented a roughened scar-like appearance, the size of which was approximately that of the diameter of the nerve. Three smaller scar-like patches occurred below, and slightly medial to the principal one. No nerve fibers could be traced within the skin. The whole appearance of this nerve termination seems exactly what might have been expected if the nerve had penetrated the skin and its external part had subsequently sloughed off, thus leaving a scar with the nerve firmly attached. The proximal part of this nerve was attached to the right wall of the cavity through which it coursed to the extra legs in company with the two main blood-vessels. This attachment was made by strands of tissue chiefly to the middle portion of the small opening. The portion of the nerve from the cyst forward consisted of a hollow, circular strand of tissue that tapered down almost to nothing. There remained no connection with the spinal cord. This nerve probably represented fused right and left medial sciatic nerves.

CONCLUSIONS

Viewing the double portion of this dog, it is seen that the left component is more fully developed and that it is nearly in normal position, while the right component is entirely at the right of the median plane. The blood-vascular, the digestive, and the urogenital systems, excepting the kidney, and the fusions and articulations of the pelvic limbs, all consistently support an interpretation of this monster in terms of a side-to-side pelvic fusion of twin primordia, with complete resorption of the pre-diaphragmatic portions. A variant of this interpretation might be based upon the supposition that an original unpaired embryonic disc suffered a caudal splitting to the point including the primordia of the pelvis. It is not possible with the available data to decide finally between the suggested alternatives of fusion and splitting. However, the mixed character of the abdominal viscera (e.g., single kidney, double colon) seems to favor the interpretation of fusion rather than of splitting. The

one chief objection to the interpretation of lateral, as opposed to dorsoventral, fusion is the presence of the unpaired sciatic nerve of the extra two legs. If the interpretation of lateral fusion is accepted, then the compound sciatic nerve seems to be greatly displaced. The sciatic nerve normally passes through the pelvic mouth and then courses laterally over the acetabulum on down the leg. The sciatic nerve of the right and left lateral legs followed this normal course. The fused sciatic nerves of the supernumerary limbs, however, entered the pair by a single root, having passed thither between the two medial acetabula, and not, as normally, through their respective pelvic mouths. The apparently ectopic position of the fused sciatic nerves can be explained on the very probable supposition that the primordia of the originally paired medial sciatic nerves fused before the medial components of the pelvis had developed beyond their blastemal stage. This explanation becomes the more plausible when it is recalled that the fused sciatic nerves had suffered degeneration at their proximal ends, due in all probability to pressure here following the further development and subsequent fusion of the two medial components of the right and left pelvis.

This dog belongs in the category of duplicate monsters designated dipygus dibrachius tetrapus, and corresponds in general to the six-legged rat recently described by Conrow¹ and more closely to certain human monsters described under this designation by Broman.²

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- 1 CONROW, SARA B. 1917 A six-legged rat. *Anat. Rec.*, vol. 12, p. 365.
- 2 BROMAN, IVAR 1911 Normale und abnorme Entwicklung des Menschen. Bergmann, Wiesbaden, S. 190.

PLATE 1

DESCRIPTION OF FIGURE

- 1 View of dog from left side, after death. Photograph by Dr. H. P. Hipp.

SIX-LEGGED DOG
JOHN SHELTON HORSLEY, JR.

PLATE 1



PLATE 2

DESCRIPTION OF FIGURES

2 and 3 Roentgenogram by Dr. H. P. Hipp.



PLATE 3

DESCRIPTION OF FIGURES

4 Drawing of the double bony structures in the pelvic region viewed from the right side. *A*, left medial femur; *B*, right medial femur; *C*, left medial tuber ischii; *D*, right medial tuber ischii; *E*, right lateral tuber ischii; *F*, right lateral femur; *G*, left lateral femur; *H*, right lateral ilium; *I*, left lateral ilium; *J*, fused medial ilia; *K*, fifth lumbar vertebra; *L*, caudal vertebrae; *M*, right deformed sacrum; *N*, small piece of bone articulating with right deformed sacrum and right lateral ilium (possibly remnant of a second vertebral column). Four-fifths life size. Drawn by Helen Lorraine.

5 Drawing of the double bony structures in the pelvic region from a caudoven-tral aspect. *A*, left medial femur; *B*, right medial femur; *C*, mouth of right pelvis; *D*, central point of the fusion between the right and left pelves, which extends along the pubo-ischial symphysis of each; *E*, left lateral obturator foramen; *F*, right lateral femur; *G*, left lateral femur; *H*, sixth lumbar vertebra. Four-fifths life size. Drawn by Helen Lorraine.

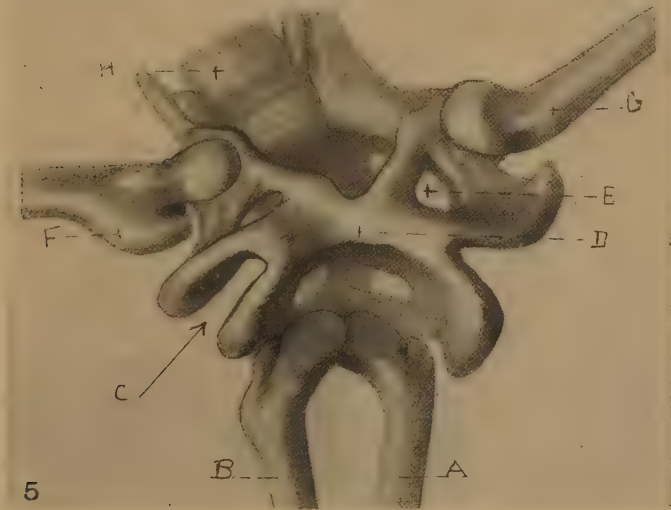
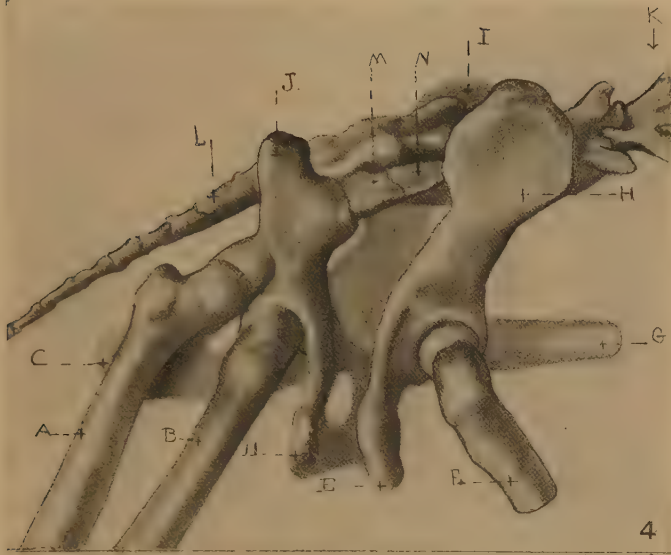


PLATE 4

DESCRIPTION OF FIGURES

6 Drawing of the anastomosis of the small intestine with the right and left colons from a right ventral aspect. The right caecum with its associated appendix is also shown. The portion of the right colon here shown represents only one of the two sacculations that were present. The second was approximately the same size. Four-fifths life size. Drawn by Helen Lorraine.

7 Drawing of the anastomosis of the small intestine with the right and left colons from a left ventral aspect. The left caecum with its associated appendix is also shown. Four-fifths life size. Drawn by Helen Lorraine.

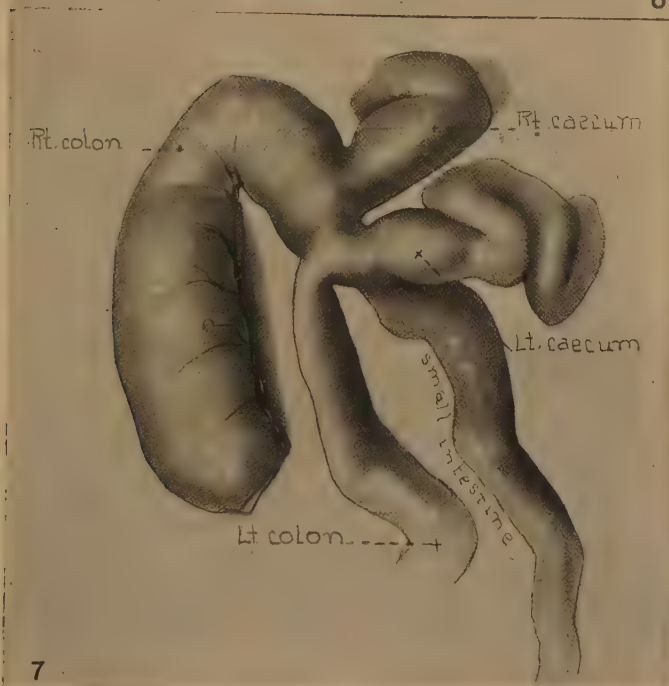
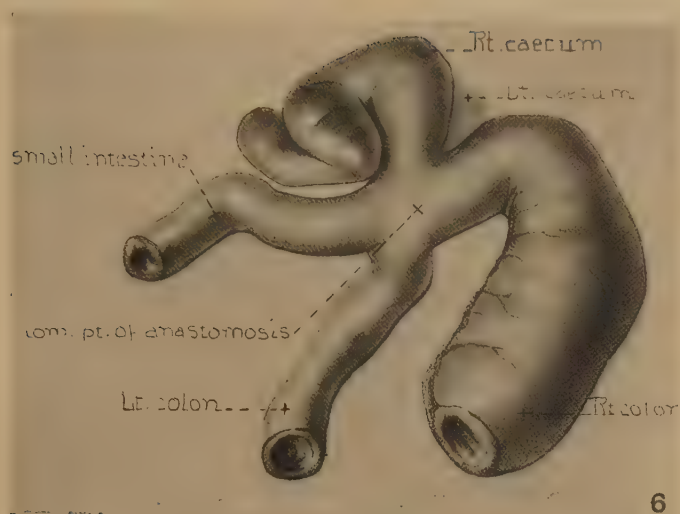


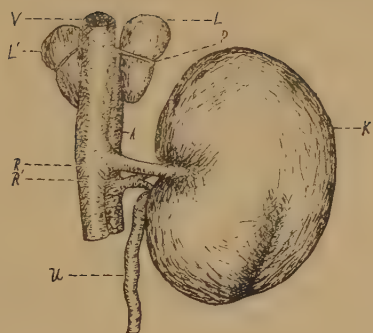
PLATE 5

DESCRIPTION OF FIGURES

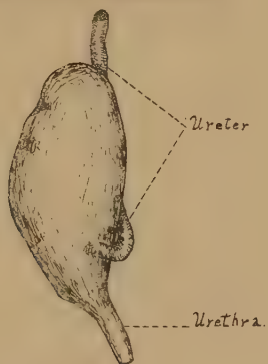
8 Drawing of the ileocolic valve from the right side. The ileum and right colon are slit open longitudinally. Four-fifths life size. Drawn by Helen Lorraine.

9 Drawing of ventral view of kidney with its blood-supply, showing also the two adrenals. *K*, single kidney of left side; *L* and *L'*, left and right adrenals; *U*, single ureter leading to left urinary bladder; *A*, abdominal aorta; *V*, inferior vena cava; *R* and *R'*, renal vein and artery; *P*, phrenico-abdominal vein. Branch of renal vein to left ovary and uterine tube not shown in this drawing. Four-fifths life size.

10 Drawing of left urinary bladder partially distended. The bladder is in a position to show the ureter emptying on the dorsal surface. Four-fifths life size.



9



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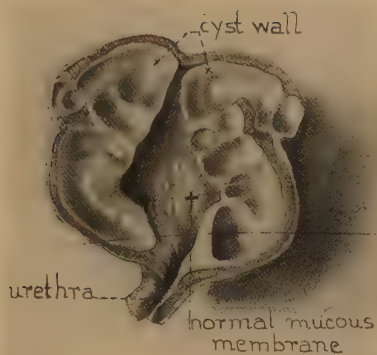
PLATE 6

DESCRIPTION OF FIGURES

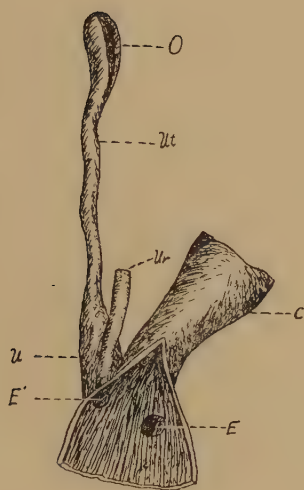
11 Drawing of the interior of the right urinary bladder from a dorsal aspect. It is slit open dorsally in the longitudinal plane. Four-fifths life size. Drawn by Helen Lorraine.

12 Drawing of the cloaca and genital organs of the right side. Cloaca is slit open. *O*, right ovary; *Ut*, right uterine tube (unpaired horn of right uterus); *U*, body of right uterus; *Ur*, urethra from right bladder; *E* and *E'*, orifices of uterus and urethra into common exit chamber forming the cloaca; *C*, right colon. Four-fifths life size.

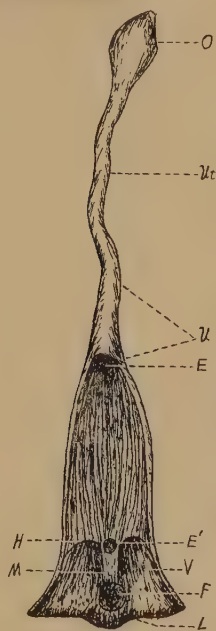
13 Drawing of the genital organs of the left side. Vulva, vagina, and uterus (in part) are slit open. *O*, left ovary; *Ut*, left uterine tube; *U*, left uterus; *E*, external uterine orifice; *H*, hymen; *E'*, external urethral orifice; *V*, vulva; *M*, central projection of fold of mucous membrane which conceals the clitoris; *F*, fossa clitoridis; *L*, labia vulvae. Four-fifths life size.



II



12



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PLATE 7

DESCRIPTION OF FIGURES

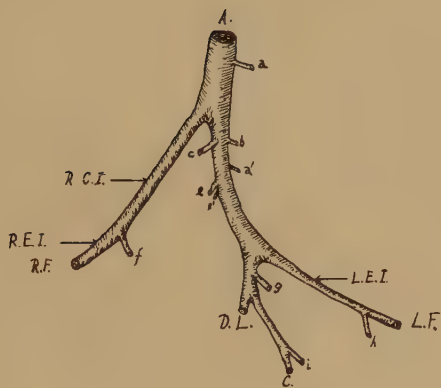
14 Diagram of the arrangement of the nipples. Each small black dot represents a nipple. One-fifteenth life size.

15 Diagrammatic drawing of the distal portion of the abdominal aorta and its branches seen from a ventral view. *A*, abdominal aorta; *R.C.I.*, right common iliac; *R.E.I.*, right external iliac; *R.F.*, right femoral to right lateral leg; *L.E.I.*, left external iliac; *L.F.*, left femoral to left lateral leg; *D.L.*, artery to extra pair of legs; *C*, caudal artery to the tail; *a* and *a'*, arteries to neighboring lymph nodes and other structures; *b*, artery to dorsal abdominal wall; *c*, artery to right colon; *e* and *e'*, arteries to structures in the right and middle portions of the pelvic cavity; *f*, artery to structures in the right portion of the pelvic cavity (probably right internal iliac); *g*, artery to left urinary bladder; *h*, artery to left ventral abdominal wall (probably left deep epigastric); *i*, artery to structures of left pelvic cavity. By pelvic cavity above is meant that portion enclosed between the lateral components of both the right and left pelves. Veins accompanied the arteries.

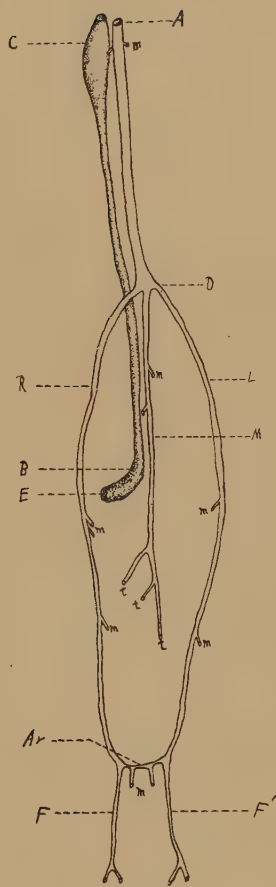
16 Diagram of the arteries and nerve of the extra pair of legs as seen from a ventral view. The nerve ran immediately behind the main artery, but in the diagram it is shoved to the right. *A*, point of emergence of artery between the heads of the two femurs; *C*, cystic enlargement on the unpaired sciatic nerve; *B*, the curve of the sciatic nerve around the medial condyle of the right medial tibia; *E*, termination of the sciatic nerve in the skin; *D*, point about 2 cm. above proximal end of fusion of two medial tibiae; *L*, lateral branch which passed around the left medial leg (also level at which the sciatic nerve passed behind the stifle-joint); *R*, lateral branch which curved around the right medial leg; *M*, medial branch which ran along dorsal line of fusion of the two medial tibiae; *A_r*, anastomosing arch on the dorsal surface of the fused medial tibiae in the region of the ankles, formed by the two lateral branches; *F* and *F'*, branches to right and left feet; *m*, small branches to the skin, fascia and scanty muscles; *t*, terminal branches of the medial branch supplying neighboring skin, fascia, and scanty muscles. Veins accompanied the arteries.



14



15



16

Resumen por el autor, Howard B. Adelman,
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Un caso extremo de espina bífida con hernia dorsal en la ternera.

El presente trabajo es una descripción de un caso en el cual una porción de la membrana mucosa intestinal emerge del cuerpo a través de un orificio situado en la región lumbar de la columna vertebral. Este defecto es una consecuencia de un defecto en la línea primitiva.

Translation by José F. Nonidez
Cornell University Medical College, N. Y.

AN EXTREME CASE OF SPINA BIFIDA WITH DORSAL HERNIA IN A CALF

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TWO FIGURES

The foetus forming the subject of this note is a part of the collection in obstetrics of the New York State Veterinary College and was submitted to me by Dr. B. F. Kingsbury for an explanation of the striking and unusual anomaly which it presents. I was unable to find an exactly similar case in the literature of teratology.

The cases found in the literature which are to some extent analogous to the one about to be described are by Gurlt ('77), who gives an account of a calf embryo with a lateral prolapse of the abdominal viscera through the spinal column; Veraguth ('01) described a human embryo with ectopia of the spleen and intestines. Finally, in 1917, Williams described a calf with the omasum and spleen extruded from an opening in the occiput. In all these cases the spinal defect is in or near the cervical region, while in the calf here described the defect occurs in the lumbar region.

Unfortunately, the head and extremities of the specimen which I describe were removed before it was brought to the museum. The musculature was removed and only that part of the vertebral column and viscera shown in figure 1 remained. No clinical history of the case is available.

The specimen under consideration is a nearly mature calf foetus which exhibits two well-marked defects: 1) an extreme degree of spina bifida and, 2) a well-marked dorsal hernia.

The cleft in the spinal column is complete and involves the entire lumbar region. X-ray photographs show that the six

lumbar vertebrae are affected and that halves of these arch around both sides of the defect, producing a somewhat triangular vertebral fissure, 7 cm. long and 3 cm. wide at the cephalic end. However, the area of complete spina bifida extends for only 2 cm. from the cephalic end of the defect; caudal to this point merely the vertebral arches are separated.

The vertebrae are more or less fused, especially in the cephalic end of the defect, where a bony prominence on the ventral side of the specimen gives evidence of this fusion. The tip of the transverse process of the sixth lumbar vertebra on the left side

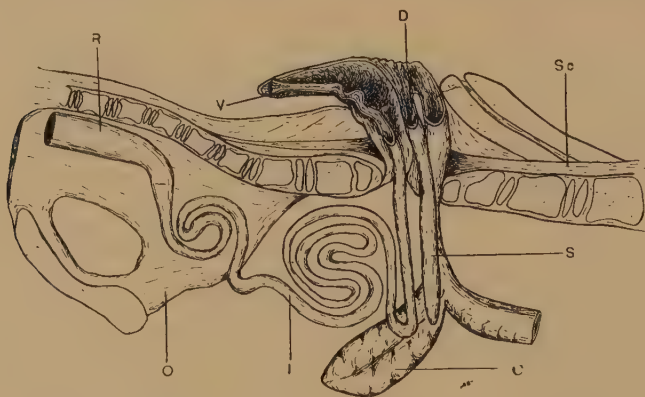


Fig. 1 Idealized sagittal section of foetus to show the relations of the intestines. *C*, caecum; *D*, dorsal opening of the intestinal pad; *I*, intestinal pad; *O*, os coxae; *R*, rectum; *S*, blind sac; *Sc*, spinal cord; *V*, ventral opening of intestinal pad.

lies under the innominate bone. The spinal cord is divided, the resulting halves passing around the defect. Nerves are given off on each side.

A pad of intestinal mucous membrane protrudes through the opening in the spinal column. When sectioned, this pad proved to be mucous membrane of the large intestine. Two openings in the mucous membrane, one dorsal and one somewhat ventral, communicate with the large intestine (fig. 1). The dorsal opening is the larger and communicates with a small portion of the large intestine posterior to the caecum and with a blind pouch which also proved to be a portion of the large intestine when

examined under the microscope. The remainder of the large intestine, that is, the portion extending from the anus to the pad, ends in a small opening on the ventral side of the caudal end of the pad.

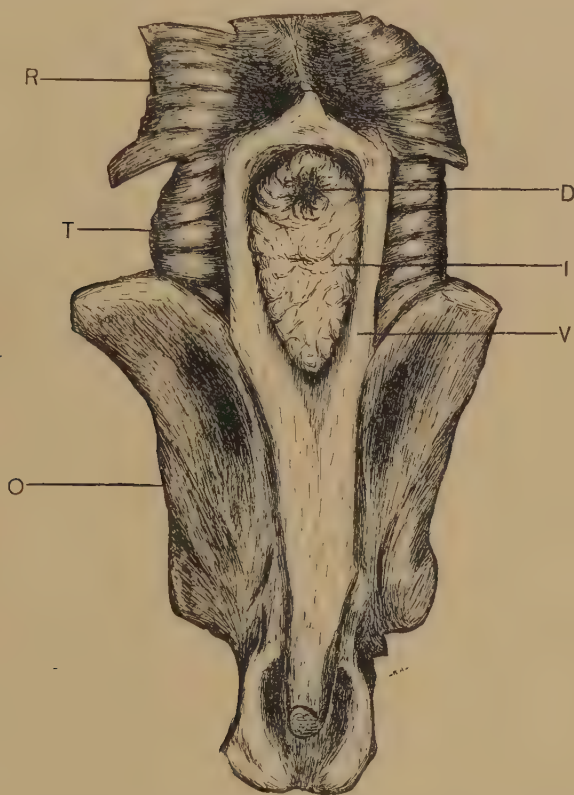


Fig. 2 Dorsal view of the defect, showing the relations of the intestinal pad. *D*, dorsal opening of the intestinal pad; *I*, intestinal pad; *O*, os coxae; *R*, rib; *T*, transverse process of lumbar vertebra; *V*, vertebral column.

The literature dealing with the causes of spina bifida is most extensive and the theories advanced are numerous. The theories of maternal impressions and amniotic adhesions need only be mentioned here. The first has long been discarded and the latter theory has also been looked upon as invalid. Gurlt ('77),

in assigning a cause for the condition which he describes, mentions the adhesions of the membranes caused by tearing due to turning of the foetus. This is a rather vague explanation at best. Modern investigators would more likely agree with Mall, who says: "Since monsters are produced in animals without an amnion, it would be well, it seems to me, to relegate the amniotic theory of the production of monsters into the class into which that of maternal impressions has fallen."

Of more importance, it seems to me, are the theories which regard a disturbance of growth metabolism as the causative factor in producing abnormalities. The experiments of Hertwig, Morgan, Stockard, and others may be briefly mentioned.

In 1892 Hertwig published his classical essay on "Urmund und Spina Bifida," in which he showed that spina bifida could be produced by the action of morphine. Morgan, in 1894, produced spina bifida by adding 0.6 per cent sodium chloride to the water in which eggs were developing. Hertwig, in 1896, found that salt solutions stronger than 0.6 per cent retarded development and the eggs died without going beyond the gastrula stage. Similar results were obtained by Hertwig and Morgan by raising the temperature of the water.

Godlewski ('97, '00, '01) and Samassa ('96, '98) found that spina bifida could be produced through lack of oxygen. This might easily be the case in faulty implantation.

Baldwin ('15) was able to produce spina bifida in almost every instance by treating the yolk portion of the egg with violet rays. The action of the ultra rays, by destroying a portion of the yolk hemisphere, results in an upset of the balance between the differentiation of the neural canal and the approximation of the blastoporic lips. The differentiation is not retarded, and the half tubes differentiate into two tubes before the lips of the blastopore close.

In the present instance, the defect unquestionably arose very early in the development of the individual and is essentially the same as those produced by Hertwig, in whose experiments spina bifida or 'ring' embryos resulted from incomplete approximation of the blastoporic lips.

There is no evidence that gastrulation in the calf is accomplished by means of blastoporic lips, but we may regard the primitive streak as homologous with the blastoporic lips, since both give rise to spinal cord, notochord, and mesoderm. The opening, in this instance, may be a secondary condition which has arisen in the region of the potential neurenteric canal, the persistence of which has been recorded in numerous instances.

The failure of the blastoporic lips (primitive streak) to approximate closely, differentiation, however, not being retarded, results in an opening bounded by material which becomes spinal cord, notochord, mesoderm, and perhaps a small amount of entoderm. In any case, however, the latter would adhere to the edges of the opening forming a passageway into the primitive digestive cavity which may or may not coincide with the position of the potential neurenteric canal. Veraguth ('01) regards the open neurenteric canal as the cause of the anomaly which he describes.

The dorsal hernia which occurs in this specimen may be interpreted thus: There is a gap in the dorsal wall of the intestine at the primitive streak, and the ventral wall pushing up through the gap has produced a pad of mucous membrane such as here found. I regard the blind sac as an outpocketing caused by a fold in the intestinal wall. The steps in the formation of this dorsal hernia may be easily understood by consulting a series of figures given by Cullen in "The Umbilicus and its Diseases," page 224.

It is interesting to note that spina bifida always occurs high up or low down in the spinal axis and to speculate why the defect should be so restricted. Lebedeff's ('81) theory that the curvatures of the spinal axis disturb the normal development of the medullary tube seems to be invalidated by two facts: 1) the neural folds have already closed before the body acquires its normal curvatures and, 2) the cervical flexure is most pronounced, whereas spina bifida is most frequent in the lumbar region.

In conclusion, I wish to thank Professor B. F. Kingsbury for many helpful suggestions; Professor W. L. Williams, who loaned the specimen for description, and Mr. R. R. Humphrey, who made the drawings.

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Resumen por el autor, R. M. Strong.
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Sobre un modelo económico de los principales tractos de la
médula espinal y tallo cerebral.

Este modelo incluye dibujos de secciones transversales (aumentadas ocho diámetros) practicadas en cuatro niveles de la médula y en siete niveles del eje cerebral, montadas sobre un tablero de diez pies de longitud y un pie de anchura. Para representar los tractos mas importantes se emplean cintas coloreadas. El problema de indicar el trayecto de los tractos entre el tallo cerebral y el cerebelo se resolvió colocando un arco sobre la región del puente. En este arco se insertan los tractos con conexiones cerebelosas, representados por cordones coloreados. Los materiales empleados en este modelo suponen un gasto mínimo. Este modelo ha sido usado con gran provecho por varias clases, siendo especialmente útil para la obtención de conceptos sobre la proyección de los tractos.

Translation by José F. Nonidez
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AN INEXPENSIVE MODEL OF THE PRINCIPAL SPINAL CORD AND BRAIN STEM TRACTS

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TWO FIGURES

The apparatus described here has been useful in helping my students in the difficult work of learning the tracts of the cord and the brain stem. It is especially helpful in getting projection conceptions, and it involves little expense.

Drawings with a magnification of eight diameters were made for four levels of the cord and seven levels of the brain stem, the last being through the diencephalon. These drawings were made on light bond typewriter paper, and they were pasted on light binding board to produce what will be termed sections in this paper. In order to have the structure outlined visible on both faces of each section, a reverse copy of each drawing was made. This was accomplished by tracing the second drawing for each section on a piece of paper which was held against the back of the sheet of paper bearing the drawing. The two sheets were placed against a window pane with the first drawing against the glass. With sunlight transmitted through the two sheets, it was easy to make the tracing.

The pictures can of course be made by photography or with the aid of a projection outfit. A pantograph can also be used to advantage in getting a desirable size for the drawings.

A board 10 feet long and 12 inches wide was used as a base; it was stained and varnished. The sections were mounted on the board by means of strips of galvanized sheet iron (figs. 1 and 2). These strips were cut $1\frac{1}{2}$ inches wide by $4\frac{1}{2}$ inches long. Each strip was bent so that two limbs making a right angle with each other resulted. One of these limbs, $3\frac{1}{4}$ inches long, was fastened

to the board by screws. The other limb, $1\frac{1}{4}$ inches high, has a vertical position. Two pairs were used for each section, and they were mounted so that the vertical limbs had just enough space between them to insert the base of a section with a tight fit.

Before mounting, holes were made in the horizontal limbs for the screws used in fastening them to the board. It was not found necessary to fasten the vertical limbs to the sections as the tight fit and the strings employed in the model hold the sections in place.

There is a tendency for the sections to be pulled away from a vertical position by the taut strings. This difficulty was met by using a piece of white string as a stay line. It was attached to the top of each section at its middle and was tied at the ends of the board, after being made taut.

Colored strings were used to indicate tracts, and they were fastened at their ends to nails. A tract not extending the whole length of the cord, for instance, is represented by a string which was deflected beyond its last level in the model to a nail at one side.

Descending tracts are represented by red strings, exteroceptive by blue, proprioceptive by yellow, and association tracts by purple. The colors fade eventually and become dull from soiling, in which case it is a very simple process to substitute new strings for the old. The regions occupied by the tracts are indicated diagrammatically with corresponding colors in the drawings.

The cerebellum presented a perplexing problem in constructing the model. This was finally solved by placing an arch as seen in figure 1 over the pons region. Tracts passing through the restiform body, brachium pontis, and brachium conjunctivum are represented by strings which have the cerebellar ends attached at the top of the arch.

Decussations are represented in the drawings by the usual methods (fig. 2). In the case of the strings, the problem was solved by passing the string across the face of a section in the region of the decussation in question. The section is perforated three times by each string in such cases instead of once. The

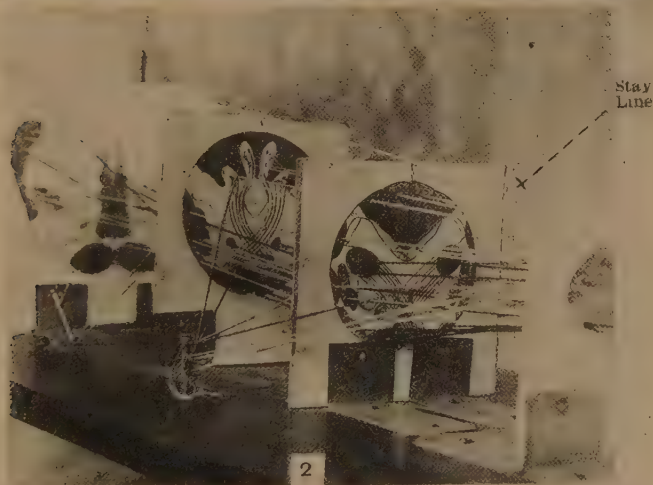
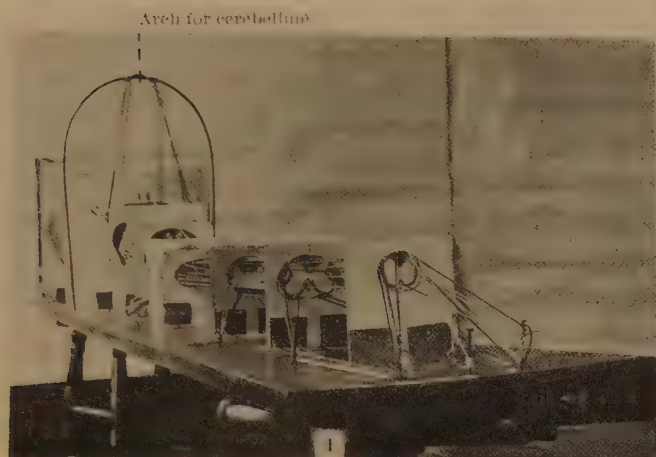


Fig. 1 View of entire model

Fig. 2 View showing region of fillet and pyramid decussations

string goes through the section before decussation back again through a second aperture and then a third time through after decussation. The same procedure was followed for the string representing the tract of the other side, and the two strings cross each other in the median plane.

Apertures in the sections were made with a steel punch before mounting on the base board. The strings were passed through the apertures with the aid of a large darning needle.

This model is large enough to permit a number of students to study it simultaneously and it is in almost constant use during laboratory periods. I have not labeled any part of it, as I prefer to have the students identify the structures represented. A limited amount of assistance in interpreting the model is given.

Resumen por el autor, Jacob Reighard.
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El almacenamiento y manejo de cuadros murales.

En vez de los listones de madera que se usan ordinariamente, el autor emplea listones de madera "basswood" teñidos con creosota. Las dimensiones de estos listones son $\frac{1}{4}$ de pulgada de espesor por $\frac{3}{4}$ de pulgada de anchura. Se clavan estos listones a los cuadros empleando clavos de alambre de $\frac{1}{2}$ pulgada de diámetro, y debajo de las cabezas de dichos clavos se perforan cuadrados de hierro galvanizado del num; 28. Los listones ocupan la superficie anterior de cada cuadro y los clavos se clavan en los lados libres. Cada listón superior lleva un gancho Hodge atornillado en el centro del listón. Cuando se hace girar al gancho de modo que venga a coincidir con el plano de la lámina, sirve para colgar esta última de una barra de hierro colocada en el cuarto en donde se guarden las láminas. De este modo éstas se conservan sin arrugas, y puesto que los listones ocupan muy poco espacio, pueden colgarse todas ellas de un modo semejante al de las hojas de un libro suspendido por el lomo. Las láminas se arreglan en orden de materias por medio de números, como si se tratase de un catálogo de materias, y cualquiera de ellas puede fácilmente sacarse y volverla a su sitio. Cuando se necesita usar una de las láminas se hace girar el gancho 90 grados, y entonces puede colgarse de un bastidor, alambre o cualquier otro soporte en la clase. Algunos de los mecanismos descritos han venido usándose hace largo tiempo; otros son nuevos. Sirven para coleccionar láminas de todos los tamaños en un espacio mínimo y para poderlas guardar en orden y emplearlas invirtiendo el menor tiempo posible. El presente trabajo indica donde pueden obtenerse los materiales empleados y su coste.

THE STORAGE AND HANDLING OF WALL CHARTS

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FOUR FIGURES

The maker usually supplies charts with wood rods tacked and glued to the ends. In use they are hung from hooks on the wall of the lecture room by means of two metal rings tacked to the upper rod. When stored they are rolled and tied about with tapes. In the Zoology Laboratory of the University of Michigan we have tried probably every known device for the storage of rolled charts. They may be piled on racks such as once were used at Harvard University. To make these, pieces of round iron, some 30 inches long or more, are bent for a couple of inches at the ends, flattened and drilled at the middle, and screwed horizontally to wooden uprights to as to project on both sides like large coat hooks and form two ladder-like sets of supports. On two such uprights, properly spaced, one may store many charts and classify them roughly. The uprights may be built on a base with casters beneath it and the whole contrivance wheeled from place to place. Labels may be written on discs of cardboard tacked to the ends of the chart rollers. As the charts accumulate and are piled several deep on each support, it is impossible to keep them in order and much time is wasted in locating and reading the small labels. In spite of the most ingenious labeling it is often necessary to unroll the charts to find those that are suitable, and this entails not only loss of time, but damage to the charts.

To find the charts more readily, we have tried supporting them on pairs of large iron hooks screwed into vertical wood strips nailed to the walls of the lecture room. The charts then lie in one plane like the rungs of numerous ladders set against the wall. They may be classified and labels put beneath the groups. But

as the collection grows it takes much wall space. It may become necessary to climb to reach the uppermost charts and they have still to be unrolled.

In place of supporting the rolled charts on metal rods, one may use deep wood frames divided into compartments like the boxes in a post office. These may be arranged to hold the charts in vertical or horizontal position, but we have found this plan as cumbersome and wasteful of time as the other.

Home-made charts accumulate in every laboratory and are apt to be of various sizes and of material that deteriorates if kept rolled and frequently unrolled. To avoid the labor of attaching them to rollers, one is tempted to let them lie flat, and we have piled them thus in large cases with numerous close-set shelves on which they may be roughly classified. It is not easy to label such charts so as to find readily what is wanted, and in pulling one from a pile for examination it is likely to be torn or damaged by rubbing. To return it to its proper place the whole pile must be taken out. Naturally one puts the chart back on top of its pile or on top of some other pile and the whole collection is thrown into confusion. In addition to this, if some charts are kept flat and others rolled, there are two places to look and time is wasted in the search.

In hanging the charts for use the two rings at the top must be put over hooks on the wall of the lecture room. To accommodate the unequal spacing of the suspension rings of different charts, the hooks must be movable. One may suspend picture hooks from a molding or wire and slip them along until the suspension rings of the chart will go over them and one must climb a ladder to do it. One may dispense with the ladder by using a wooden frame filled with wire netting and arranged to be raised and lowered by ropes and pulleys. The picture hooks may be stuck into the lowered netting at suitable intervals, the chart rings slipped over them, and the whole thing hoisted, or one may cover the hoistable frames with cotton cloth and pin or clip his charts to that.

After trying most of the plans outlined, we sought a means of keeping all charts in a minimum space in one collection with-

out rolling them and so that they could be classified and examined and each removed and returned without disturbing the rest. We sought also the easiest way of hanging them for use. The result combines the unpublished devices of friends with some of my own. The universities in which I have seen some of these devices in use are indicated in parenthesis. I do not know that any other consistent scheme has been described in print.

We now store all our charts together by hanging them from a piece of $\frac{5}{8}$ -inch iron pipe supported from the ceiling by a wire and stayed by wire to the side wall (Wisconsin). They are in a small room reserved for the purpose. The charts hang flat, one against another, like the leaves of a book. Because the wooden rods take too much room, we have removed them and have substituted thin strips of basswood (fig. 4, chart at right.) A thousand of these $\frac{1}{4} \times \frac{3}{4}$ inches by 40 inches, cut at a planing mill, now costs \$18.00. Probably any good soft wood would answer, but hardwood warps so that the strips do not stay flat. The strips are stained brown by dipping in creosote. They are tacked to the face of the chart along its ends by means of $\frac{1}{2}$ -inch wire tacks or clout-nails set from 4 to 6 inches apart and clinched on the free face of the strips. To keep the heads of the nails from tearing through the charts we have put under each a piece of 28-gauge galvanized iron. This is $\frac{1}{2}$ inch square, perforated at the center, and has the corners turned with pliers to as to form small points that penetrate the chart and go a little way into the wood. We find it better not to use glue, and none of our charts attached to the strips by tacks in the manner described has yet come loose from its supports. A piece of sheet iron 2 x 2 feet now costs fifty cents, and from it about 1000 squares can be made in the laboratory.

For suspending the charts we use the hook devised by Prof. C. F. Hodge. It is screwed into the upper strip at such a point as to make the chart hang level. When the hook is turned into the plane of the chart it serves to suspend it from its support in the chart room as a suit of clothes is hung from a rail (fig. 1). When the chart is to be used, the hook is turned through 90 degrees and may then be slipped over a picture molding, wire, or other

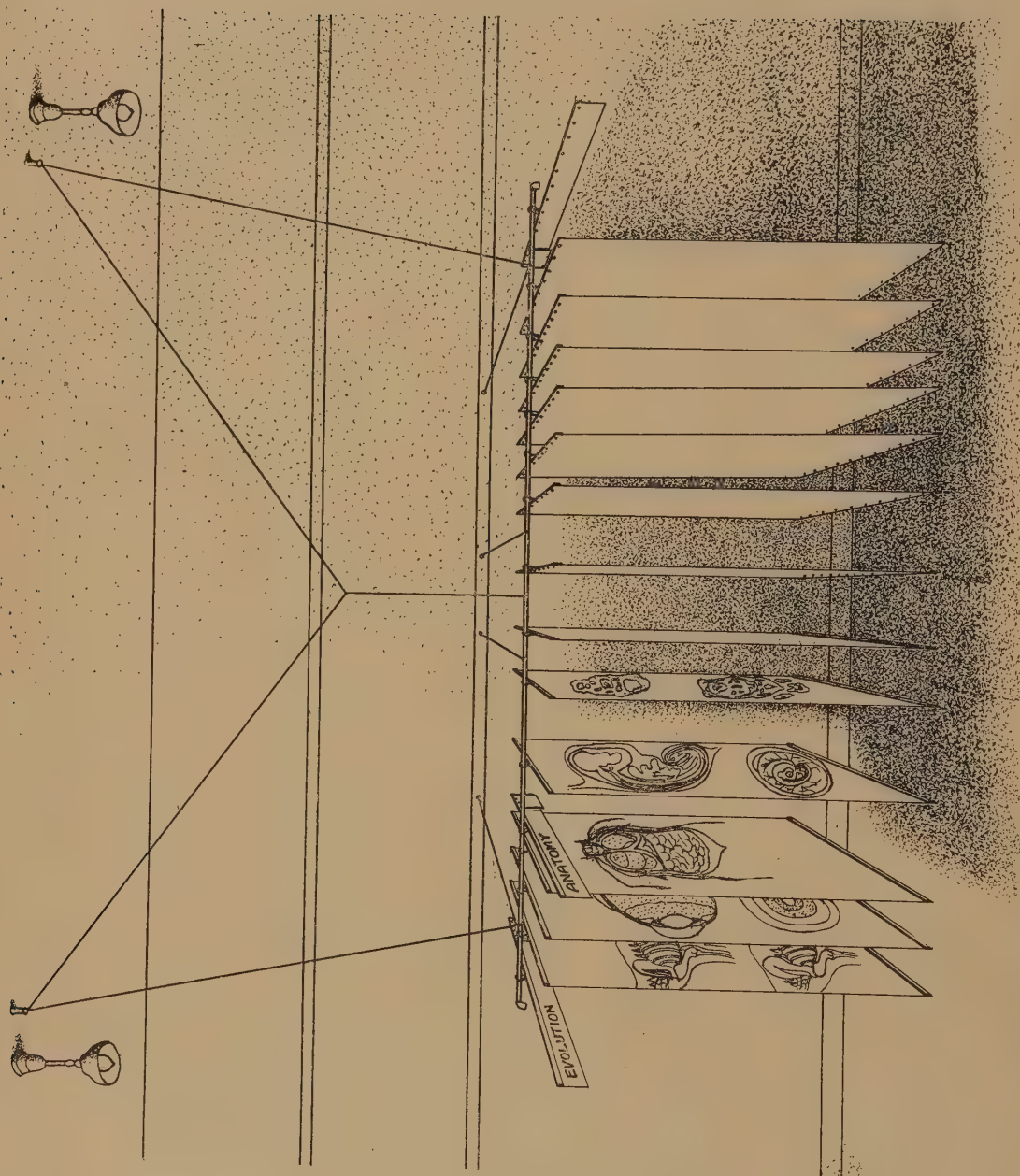


Fig. 1 Showing charts hung from an iron pipe in the chart room. The pipe is suspended from the ceiling and stayed to the wall by wire. Each chart is hung by a single Hodge hook.

support in the lecture room. To hoist it into place and get it down again, we use a light wood pole $6\frac{1}{2}$ feet long, also Professor Hodge's device. At one end the pole is provided with a ferrule through which is driven the sharpened end of a piece of $\frac{3}{8}$ -inch round-iron. This is bent as shown in figure 3 and has its free end slotted to form a pair of claws like those on a tack-hammer. The hump on the suspension hook fits between the

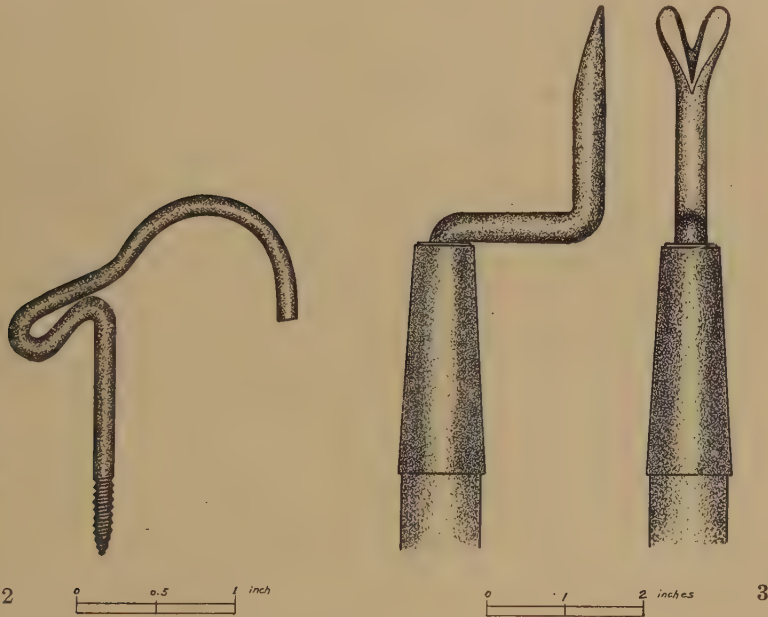


Fig. 2 The Hodge hook. See text

Fig. 3 Pole for putting up and taking down charts. For description, see text

claws on the pole and permits the chart to be handled without waste of time. In each lecture room a short suspension rod is provided. To this the charts are transferred after use and from it an assistant collects them from time to time and returns them to the chart room. The Hodge hooks were obtained from the Wire Goods Co., Worcester, Massachusetts, and cost, before the war, \$1.35 per gross. The iron claw may be made by any blacksmith.

For displaying charts in the lecture room we have used a modified form of a device made for displaying buggy robes, and used for charts at the University of Wisconsin. As used by us, this device consists of eighteen wood arms, each supported by an iron rod, and arranged to swing like the arm of a derrick (fig. 4). The arms are pivoted to steel sectors which turn on the central upright axis. By turning the sectors all the arms may be thrown either to right or left. Each arm supports two charts back to back. Any one of these may be brought into view by turning the arms as one turns the leaves of a book held vertically. The device may be attached to the wall, as ours is, or carried on a movable base resting on the floor. It may be obtained from John Best, Galva, Illinois, and cost (in 1915) \$19.00.

The whole arrangement has proved very satisfactory. The charts are designated by the numbers of the Concilium Bibliographicum gummed to the upper wood strip (fig. 4). They are arranged on the rail in systematic order, and any one may be located, removed, inspected, and returned to its place without difficulty. To subdivide them, index labels are hung at intervals (fig. 1). These are wood strips suspended from the rail by Hodge hooks. They project beyond the charts at one end and each bears at that end a square of chart cloth with an appropriate label and at the opposite end a thin bag of sand to balance it. Charts of any ordinary size may be accommodated. Very large maps may have to be kept rolled in a separate place, but they may be represented in the chart collection by appropriate dummies on which are written references to their location and to which may be attached photographs of them. Our collection consists now of 310 charts varying in size from 2 x 2 feet to $5\frac{1}{2}$ x 3 feet and made of various materials. These occupy in storage a space 11 feet long, but the same space will probably accommodate nearly twice as many and still permit anyone to be examined in situ. If longer hooks were used the charts could be hung alternately high and low from parallel supports so that the wood strips would not be opposite. The same space would then accommodate many more,

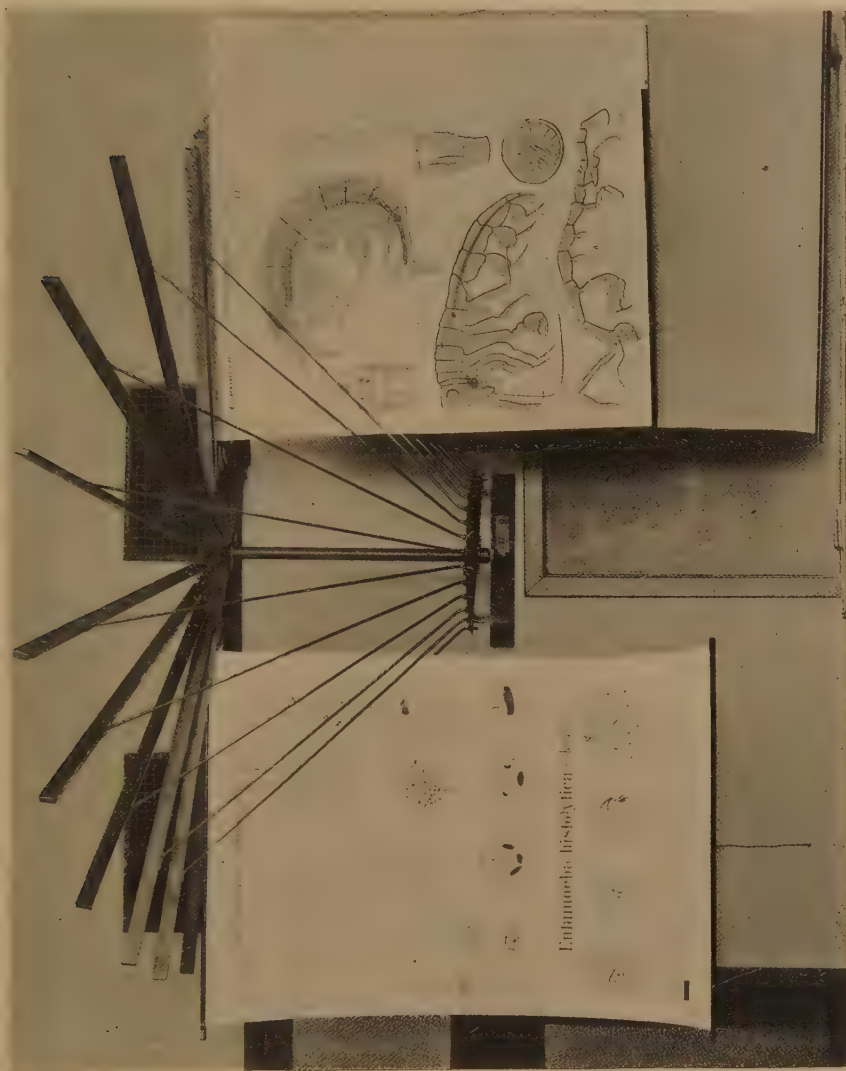


Fig. 4 The Best chart hanger for thirty-six charts, see text. The smaller chart at the right shows the basswood strips. The other two have the usual wood rollers. Note the place numbers on the upper strip.

As our collection grows we shall make a card catalogue of the charts in which each chart will be represented by small photographs (Pennsylvania). By attaching concilium numbers to the duplicate photographs and arranging them according to the concilium system, cross references will be made to many of the charts. Thus the chart shown at the right in figure 4 would be represented in the catalogue by several photographic cards, each of which would bear an identical number to show the location of the charts in the collection. These cards would bear also distinctive concilium numbers by which they would be placed in the catalogue under crustacea, embryology, and under one or more anatomical designations.

Resumen por el autor, Roy Lee Moodie,
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La naturaleza del sistema Haversiano primitivo.

Los huesos mas antiguos, encontrados en el Silúrico y el Devónico, carecen de verdaderos sistemas Haversianos, que se desarrollan primeramente con cierta extensión en Dinichthys, del Devónico. En este pez acorazado alcanzan el máximo de desarrollo en conexión con el proceso dentario de la maxila y premaxila. Las lagunas participan de la naturaleza de los ódontoblastos; los canalículos nunca comunican entre sí; la laminilla fibrilar existe; las fibras perforantes no se han desarrollado; el canal central es ancho. El polariscopio es útil para distinguir la naturaleza de los sistemas Haverísanos primitivos. No existen pruebas sobre la evolución de la estructura del hueso; se percibe un cambio bastante brusco con la introducción de las formas de mamíferos.

Translation by José F. Nonidez
Cornell University Medical College, N. Y.

THE NATURE OF THE PRIMITIVE HAVERSIAN SYSTEM

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ONE PLATE (THREE FIGURES)

The term Haversian system is necessarily of very general significance and is used in a broad way to distinguish any concentric arrangement of osseous lamellae around a central canal. It is often difficult to distinguish between a dentinal system, that is, a concentric arrangement of dentine, around a dentinal tubule and a true Haversian system as seen in long bones, since the two often grade into one another. The presence of lacunae does not seem to be essential to an Haversian system, though they usually are present. In the fishes, both modern and ancient, osteoid tissue, largely lacking lacunae, may arrange itself around a vascular opening and thus have all the appearances of an Haversian system, and give the same orthorhombic light reactions under polarized light.

The type of such a system may be taken as those most highly specialized Haversian arrangements seen in the long bones of man, especially in the femur. From this complete system down to a slight lamellar arrangement of substances one may find all gradations in a series of fossil bones representing the history of the vertebrates from the Devonian to the Pleistocene. Such a review has been made, and it will doubtless be of interest to describe and illustrate the most ancient Haversian system of which we have any knowledge.

There is no apparent indication of a gradual evolution in form of the Haversian system from the most ancient vertebrates to modern mammals, although there is a gradual development in the form of the lacunae and canaliculi. The reptiles do not

show a higher type of Haversian system than do the amphibians or fishes, as they do in their skeletal organization. Haversian systems in dinosaurs are as primitive as they are in Devonian fishes. They seem to have sprung into existence full formed without undergoing the process of evolution such as has obtained in the bodily organization of the vertebrates.

The most ancient organization of osseous elements which simulate an Haversian system are to be found in the dental process of the premaxilla of a Devonian arthrodire, *Dinichthys* (figs. A and B), allied by some paleontologists with the lung fishes. This arrangement is well known to paleontologists and has been described by Clappole (94). These curious structures are not present in other portions of the armor of *Dinichthys* and are to be regarded as specialized dentinal systems, though not found in the true teeth which are not connected with the cranial skeleton. The Haversian canal resembles a dentinal tubule, the lacunae are those seen in the cementum of modern fishes, the lamellae are fibrillar and partake of the characteristics of dentine as seen in the teeth (fig. C) of Carboniferous sharks, the interlamellar space is filled with cement and there are true interstitial lamellae, though never any of the type due to the partial absorption of other Haversian systems. I have not seen this type, known as false interstitial lamellae in any fossil vertebrate. The orthorhombic light reaction under polarized light is exactly like that of the highly specialized Haversian systems in the femur of man. The canaliculi from the lacunae communicate neither with each other nor with the central canal, nor do they do so in any fossil vertebrate below the mammals. The lacunae are not confined largely to the interlamellar spaces, as they are in mammals, nor is there any apparent plan in their arrangement. Often, as in a Permian reptile, one finds three lacunae grouped together, surrounded on all sides by wide areas of osteoid tissue lacking lacunae.

The use of polarized light is essential to an adequate understanding of the structure of fossil bone, since usually under polarization, lamellae, fibrillae, canaliculi, and other minute histological units, invisible under ordinary light, stand out with

startling distinctness. The importance of this has been commented upon by various authors in their studies on the histology of fossil structures.

Arey ('19) has recently called attention to the presence of Haversian systems in the membrane bones of man. The systems he described and figured, however, cannot be called true Haversian systems, but resemble those seen in fossil reptiles. It is interesting to note in the temporal bone of an Oligocene mammal an arrangement of substances exactly similar to those described by Arey for man. These intermediate or pseudo-Haversian systems often fail to give an orthorhombic light reaction, as they do in the case of the Oligocene mammal. The difference between the true and the intermediate types of systems is to be found in the absence of intercommunications of the canaliculi with either the central canal or other lacunae and in the occasional failure to secure the same light reactions. In all other respects they are similar.

The review was undertaken with the idea of gaining a conception of tissue organization in ancient vertebrates so that I might judge as to the disturbing effects of pathological processes upon the structure of the part. The presence of osteoid tissue in ancient vertebrates is a normal condition. Kolliker ('57) noted that many fish bones are composed entirely of osteoid tissue. One interesting effect in pathological conditions of fossil bone is to stimulate the growth of pseudo-Haversian systems, and to increase the vascularity of the bone. The same fact has been noted by Foote ('16) in the fractured femur of a frog, where Haversian systems are ordinarily absent.

SUMMARY

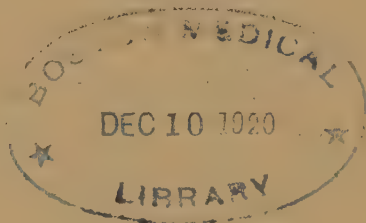
Primitive Haversian systems of the very ancient vertebrates differ but slightly from highly developed systems of modern mammals and have been but slightly modified by the passage of time. Each group of vertebrates has its own type of lacunae, but the organization of the Haversian systems remains the same. The concentric arrangement of lamellae is not an incident of

evolution, but a response to the mechanical laws of organization of the part. True Haversian systems are confined to the mammals.

A more complete account and more adequate illustrations will be found in the Williston Memorial Volume now in preparation.

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PLATE

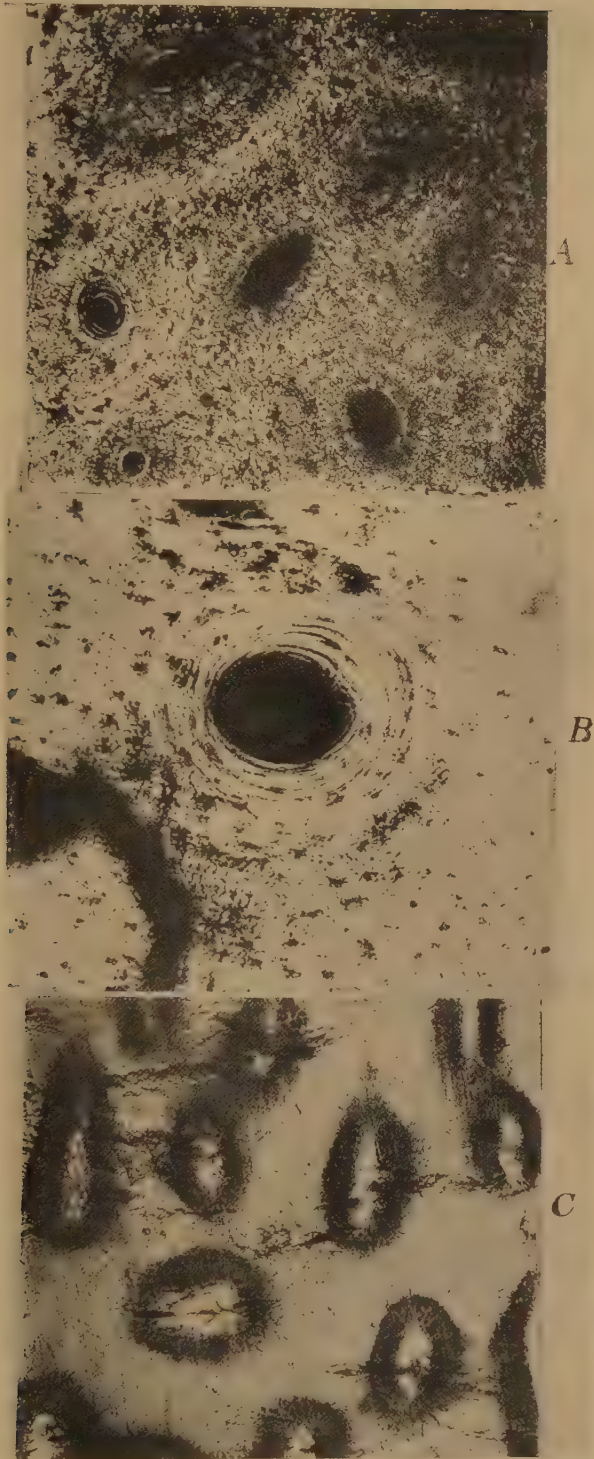
PLATE 1

EXPLANATION OF FIGURES

A A field in a section of the premaxilla of *Dinichthys*, a Devonian *Arthrodire*, showing the distribution of the oldest known representatives of the Haversian systems. Between adjacent systems are to be seen interstitial lamellae. Two systems, at the lower left-hand corner show the concentric lamellae. $\times 70$

B A single system showing large size of central canal, concentric lamellae, distribution of lacunae and nature of ground substance, which under polarized light is seen to be fibrillar. The black band at the left lower corner is a post-fossilization crack and has no significance in the histology. $\times 300$

C Dentinal tubules of *Mazodus*, a carboniferous shark, for comparison with the specialized systems in *Dinichthys* above. $\times 70$.



Resumen por el autor, Hubert Sheppard,
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Hermafroditismo en el Hombre.

En el hombre, el hermafroditismo con existencia de testículos y ovarios normalmente desarrollados en el mismo individuo aparece raras veces. En el individuo descrito en el presente trabajo los testículos aparecían en el escroto y los ovarios en la cavidad pélvica. El tejido que formaba ambos órganos era normal en estructura en todos sus detalles. Se podía distinguir perfectamente una pared muscular uterina que limitaba una cavidad que desembocaba en la vagina. Las tunicas del conducto deferente y el oviducto, así como sus cavidades podían también distinguirse. El cuello del útero ocupaba casi exactamente la posición del utrículo prostático del varón. En todos los casos de hermafroditismo se ha podido comprobar una distinción marcada entre los tejidos genitales masculino y femenino, sin encontrarse nunca una mezcla indefinida de ambos elementos (es decir, un verdadero ovotestículo). En el raro caso descrito encontramos el mismo fenómeno con una separación aun mayor de las dos clases de tejido, puesto que los testículos y ovarios ocupaban su posición normal correspondiente.

Translation by José F. Nonidez
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HERMAPHRODITISM IN MAN

HUBERT SHEPPARD

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SEVEN FIGURES

An opportunity to make a study of the anatomical structures of the genital organs of hermaphroditism in man is seldom found for two reasons: first, such irregularities seldom occur and, second, when they do occur the material is exceedingly difficult to obtain for laboratory purposes. As recently as 1911 it was asserted that "hermaphroditism in the sense that separate testicles and ovaries are found has not been demonstrated in man, nor even in other mammals beyond a doubt." We thought it worth while, in the light of this and other investigations, to report a study of the anatomical structures of an extreme case of hermaphroditism which came to the dissecting room. The gross study is supplemented by microscopical examinations in so far as the condition of the material would permit.

The cadaver featured, objectively, both as a male and as a female subject. Hair was lacking on the face and scant around the genitals, the body was large and obese, with the mammae well developed, large and flabby, which in every way resembled a female rather than a male organ. One would have judged, in so far as the external genitals were concerned, that they were male rather than female genitalia. However, upon a closer examination, one could see that there were certain irregularities. The penis was small with a dilated urethral orifice three-fourths as large as the organ itself (fig. 1). The scrotum appeared to be abnormally large, although the testicles, upon palpation, were found to be normal and symmetrically formed. When the region posterior and beneath the scrotum was palpated, its apparent unusual size was found to be due to a large fold or ridge which extended from near the anus to the pubis on either side of the penis.

THE FEMALE EXTERNAL GENITALIA

After the skin and scrotum were completely reflected from the urogenital triangle, the large ridge beneath the scrotum was found to be a structure which resembled female external genitalia. Both the labia majora and minora were nearly normal in size, the former extending to the posterior commissure, while the latter formed the frenulum. The skin and dartos of the scrotum divided into two lamina on reaching the postero-inferior part of the labia majora. The superficial layer continued as the skin and fascia of the femoral region, the inner lamina thickened into the labia majora. The minora was two membranous folds within the majora and surrounding the penis or enlarged glans clitoris. At this stage of the dissection, if one would disregard the latter enlarged organ, the cadaver was nearer a female than a male subject.

THE PENIS AND VAGINA

The penis in all respects resembled a glans clitoris which had developed into an organ that closely figured externally as male genitalia with a cone-shaped dilated urethra (fig. 1). At the large or vaginal end of the urethra was an opening that extended back into the uterus through the prostatic-cervix of the uterus (fig. 2), which will be described later. The penis was small, measuring a little more than $1\frac{1}{2}$ inch in length and $\frac{1}{2}$ inch in diameter. The glans had a prepuce fused with the erectile tissue of the corpus cavernosum, and was only a rudimentary fold at the end of the organ. The dorsal vein, arteries, and nerves were regular and similarly related as those found in a normal subject. Externally, the urethral orifice of the corpus cavernosum urethra (fig. 1), measured $\frac{3}{8}$ inch in diameter. This opening gradually increased in diameter until it was a little more than an inch in diameter at the urogenital diaphragm. In so far as we could note, there was no spongiosum tissue present in the urethral part of the organ. Both the urethra and the vagina opened into this enlarged urethra. The true urethra

itself was only about $\frac{3}{4}$ inch in length. This duct passed through the upper part of the prostatic-cervix portion of the uterus, while the vagina was located in the lower two-thirds and extended upward and backward into the uterus proper. Posteriorly, the corpus cavernosum penis divided into two short crura (fig. 1) $\frac{3}{4}$ inch in length.

THE UTERUS

The body of the uterus was separated from the bladder by the vesico-uterine fold of peritoneum in the usual manner. However, the uterus as a whole was somewhat lower down in the pelvic cavity than is ordinarily found in normal cases. This was due possibly to the development of the organs—the fusing of one genital system with the other. The greatest width of the uterus was 1.5 cm., with a total length of 5.5 cm.; the body was 4 cm., and the prostatico-cervix 1.5 cm. A uterine body cavity was perfectly developed, and measured nearly 5 cm. This cavity extended into the uterus with little demarcation between the two organs. The entire cervix was fused with the prostate; in fact, the prostate was a mere enlargement of the cervix of the inferior extremity of the uterus. The uterus held the same relation to the prostate that utriculus prostaticus holds in a normal male subject. Not only the lumen, but the uterine glands and muscular walls could be easily defined (fig. 3). The ductus deferens entered the prostatico-uterine canal of the cervix by piercing its posterior wall (fig 2). A broad ligament was well developed, resembling in every detail a normal female subject except the course of the ductus deferens, which will be described later, and it was a little thicker and wider, due to the fact the uterus was a little lower in the pelvis as has been previously described.

THE DUCTUS DEFERENS

The ductus (vas) deferens differed in no respect from a normal male subject until it passed through the annulus inguinalis abdominis in connection with a very rudimentary ligamentum teres uteri (fig. 2). It then coursed alongside, and posterolateral

to the oviduct, at first encircling the ovaries. When it reached the level of the uterus, it made a quick S-shaped turn, and entered the superior part of the cervix of the prostatico-uterus. The histological structures of the duct are very well developed. The epithelium surrounding the lumen is slightly disintegrated, as is shown by the photograph. The circular and longitudinal muscle layers are clearly defined, and in a number of sections the tunica propria and the inner longitudinal layer are also easily recognized (fig. 4).

THE OVARIES AND OVIDUCT

The ovaries measured about 1 inch in length and $\frac{1}{2}$ inch in breadth. They were attached to the mesovarium in the usual way. However, the ovaries were found to be in a poor state of preservation for histological purposes; nevertheless, some of the materials stained sufficiently well to demonstrate the ovarian tissue. One of the larger follicles as well as a number of smaller are shown in figure 5. A little below the follicles is a light area where the corpus luteum has disintegrated from the rest of the tissue.

Each oviduct took a normal course to the proximal opening into the uterus (fig. 2). The course of each duct was at first almost horizontal, lateral, and posterior from its attachment to the uterus until it reached an inferior lateral portion of the pelvic wall where it came into relation with the uterine extremity of the ovaries. Then it coursed at right angles, and passed almost vertically upward along the mesovarial border of the ovary to the mouth of the infundibulum and the fimbriated extremity of the duct. Microscopically, the sections of the oviduct very clearly differentiated the various tunics; the serosa, the longitudinal, and the circular muscle layers show with marked clearness (fig. 6). The epithelium as well as the inner part of the mucosa has somewhat disintegrated from the lumen. It was possible in many of the sections to define the epithelial cell structures. A lumen extended throughout the full extent of the duct.

THE TESTES

The testes did not differ from a normal testicle, except in size. The right testis measured $1\frac{1}{2}$ inch in length, $\frac{3}{4}$ inch in breadth and 1 inch in diameter anteriorposteriorly. The left testis was nearly the same size as the right except for length. It measured a little more than $1\frac{1}{4}$ inch. Each testis lay upon and slightly laterally to the large ridge or fold beneath the scrotum. This arrangement gave the scrotum its extremely large appearance when viewed in its normal state. The funiculus spermaticus had all of its usual structures, even the pampiniform plexus was easily worked out. A small round ligament, before mentioned, was fused with the funiculus as far as the point where the labia majora began. At this point it was lost and could not be traced any farther along the cord.

This tissue, like the ovaries, was in a poor state of preservation for histological study. However, in many of the sections the convoluted tubules could be easily differentiated (fig. 7). Only the shape of the tubule with its contents could be clearly defined. It was impossible to differentiate between sexual and sustentacular cells except in a few sections. In these better sections, a few interstitial cells could be observed under oil immersion.

DISCUSSION

According to Virchow, this individual subject would be an *individuum uterusque generis*, since both male and female organs are found almost equally developed. Klebs regards a *hermaphroditismus verus* as a subject who possesses both male and female genital organs united in it. In the specimen under consideration, we find two sets of reproductive glands. They were not united in the sense of ovitestes, but since both the ductus (vas) deferens and the oviduct (Fallopian tube) enter the uterus and, further, the round ligament and the spermatic funiculus have a union as well as a natural position and course, we can say that there was an indirect union. Even according to Kleb's definition this would be an *hermaphroditismus verus*.

Gudernatsch says that "hermaphroditism in the sense that separate testicles and ovaries are formed has not been demonstrated beyond doubt." Except for minor variations which we have previously described, we find not only separate testicles and ovaries which are in their normal position in the body, but also a complete male and female urogenital system with the exception of the urethro-vagina and the prostatico-cervix of the uterus. Here we have noted the fusion of the two systems into a single system where male and female are combined.

Such a finding as this substantiates the old theory of Waldeyer that there is a bisexual anlage of the genital ridge. We cannot quite see how Benda's theory, "that the primary anlage of the entire sexual system of the vertebrates must be regarded as female," would harmonize with facts now recorded. A separate development would seem to be further substantiated by the fact that in every case of hermaphroditism on record there is always a sharp distinction between the two kinds of tissue, and never an undifferentiated mixture of both elements, as would be the case if the germinal epithelium could produce either male or female reproductive tissue.

In every male subject the prostatic utriculus, a homologue of the vagina of the female, can be demonstrated. It would appear from what we know of the embryological development of the urogenital system that there would be a fusion of the prostate, vagina, and uterus in an hermaphroditismus verus. This would no doubt explain the variation or fusions of the two systems found in the cadaver we are considering.

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EXPLANATION OF PLATES

All the figures are untouched photographs of the organs described in this paper. Figures 1 and 2 are macroscopic photographs of the external and internal genital systems. The remainder of the figures are microscopic photographs.

PLATE 1

EXPLANATION OF FIGURES

1 A photograph to show the external genital organs. The short penis has been dissected out with its crura and laid upon the pubis. The dilated urethra has been split and pinned open to show the small opening into the vagina as it turns backward to enter the uterus.

2 A photograph of the same section from a pelvic view. The vagina and uterus have been laid open and pinned backward to the broad ligament. The ductus deferens can be seen on the right side near the upper extremity as it enters the cervix of the uterus. Near the lower extremity of the uterus can be seen both oviducts coming off from the angle of the uterus. The bladder could not be shown in the photograph.

3 A microscopic section to show the lumen and muscular wall of a portion of the uterus. This was taken from the right side 2 cm. from the cornu.

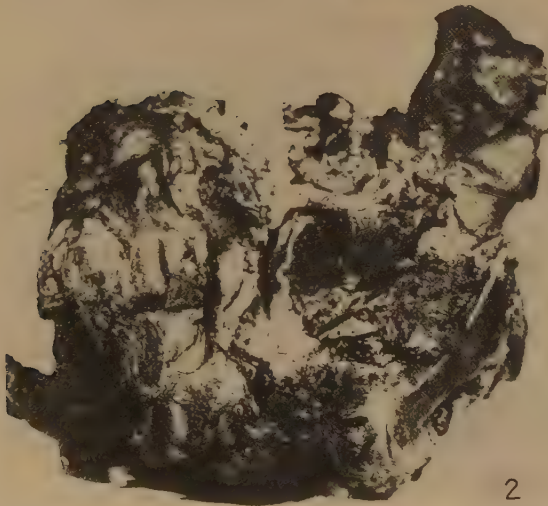
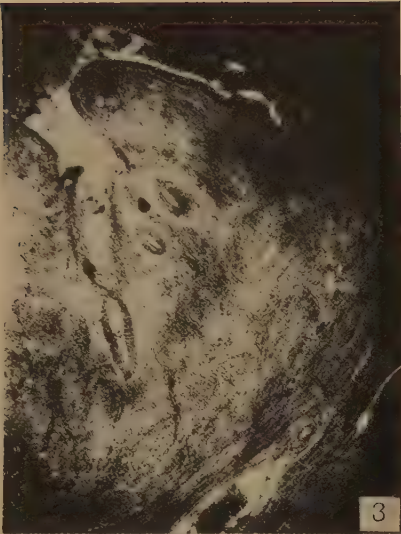
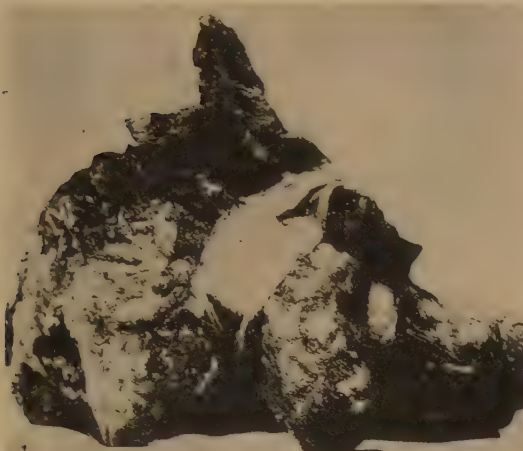


PLATE 2

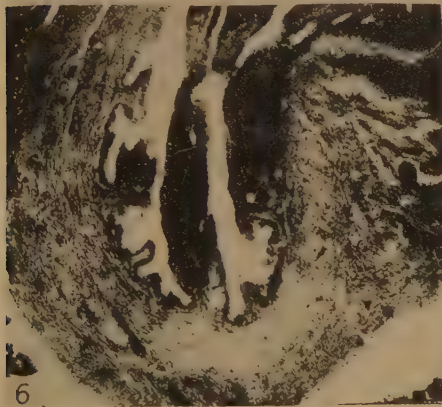
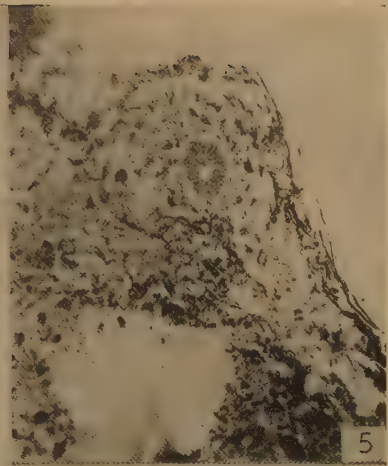
EXPLANATION OF FIGURES

4 A section of the ductus deferens to show the tunics. Considerable disintegration has taken place in the lumen. However, all the layers of the duct show clearly in the photograph.

5 A section of the ovary. A large follicle is seen near the top of the photograph. Two smaller follicles to the right can also be seen. Below and near the bottom of the photograph is a light area. This was an area of disintegrated corpus luteum.

6 A section of the oviduct taken about half-way between the ovary and the uterus.

7 A low-power section of the testicle, to show the convoluted tubules and the connective tissue among the tubules.



BOOK REVIEW

LE EMOPATIE. By Prof. Dott. Adolfo Ferrata della R. Università di Napoli. Vol. 1. Parte Generale, XVI and 1-482 pp., 21 colored lithographed plates and 8 text-figures. Milano: Società Editrice Libraria, 1918. Price, unbound, L.30.00.

This is one of the most interesting, complete, and usable books on morphological hematology ever published. It is the kind of book which unfortunately cannot be produced in this country, for no American publisher could furnish the splendid colored lithographed plates and probably no publisher in this country would publish such an extensive text on a subject which necessarily appeals to a small audience. The plates are of exceptionally high quality, and the figures are so arranged that the plates will prove very useful even for those who have difficulty with the Italian text.

The text matter is arranged very systematically, and each chapter is followed by a very extensive bibliography. Citations to literature and discussions of theories are so numerous that the book will be of great value as a reference work to anyone working in this field. It should be accessible to every laboratory in which there is an interest in hematology.

The book is far more than a compilation of the work of others, for there is a hardly a phase of the subject to which the author has not contributed by his own researches, the results of which have appeared in numerous previous publications. The work is really an extended résumé of Ferrata's own work and that of his students and collaborators, Di Guglielmo and Negreiros-Rinaldi. Of special value is the fact that it has been possible to include the results of most recent research in this field. It is thus the only place where one will find a summary of much of this work.

The chapter on technique, to which the first eighty-four pages are devoted, gives a very complete account of the modern methods of counting, haemoglobin estimation, fixation and staining of blood smears and of the blood-forming organs, with considerable space devoted to the methods of supravital staining of fresh blood and the making of permanent preparations of blood smears stained in this manner.

Part II, sixty-three pages and eleven plates, deals with the red blood-cells. The results of supravital staining, the maturation of the red corpuscle, and the pathological morphology of erythrocytes, including polychromatophilia, basophilic punctation, Howell-Jolly bodies, etc., are prominent features of this section. Sixteen pages are devoted

to the discussion of basophilic punctation. In regard to the origin of the basophilic granules it is to be noted that Ferrata has given up his former view that they are derived from the parachromatin of the nucleus. With Pappenheim and Askanazy he now agrees that they are of cytoplasmic origin. His general conclusion in regard to basophilic granulation is that it represents a phase of maturation of normal erythrocytes in certain periods of embryonic life; it is atypical for the adult, and morphologically it corresponds to the basophilic substance of the primitive lymphoid erythroblast. In the normal adult the erythrocyte passes through a polychromatophilic phase in order to reach its final acidophilic state, but in pathologic conditions of the adult 'conglobation' of the basophilic substance during the polychromatophilic stage gives origin to the basophilic granules. Clinically, basophilic granules appearing in more or less severe types of anemia indicate a return of the mechanism of maturation of the erythrocyte to an embryonic type. In this connection it must be remembered that Ferrata's previous researches have shown that a condition analogous to basophilic punctation is a normal phase during the maturation of the erythrocytes of early mammalian embryos.

Several plates are devoted to illustration of the maturation of the erythrocyte and megalocyte. The numerous exceptionally clear figures include all important stages in the differentiation of red cells from the 'hemocytoblast' (primitive progenitor of all the granular leucocytes and erythrocytes) to the fully matured non-nucleated orthochromatic erythrocyte. Ferrata and Negreiros-Rinaldi have been successful in recognizing the very earliest stages in the differentiation of the red-cell series in a cell-type which they have named 'proerythroblast.' This cell retains the nucleoli of the 'hemocytoblast' ('lymphoidocyte' of Pappenheim), but shows some slight differences in other respects. The chromatin network is somewhat coarser and the light spaces between the chromatin strands are more sharply defined. The cytoplasm is more homogeneous and more basophilic and does not show the spongy differentiation of the primitive stem-cell. This cell is inserted between the lymphoid hemoblast of Pappenheim and the stem-cell. For the megaloblast a similar stage is recognized—the promegaloblast.

Part III, pages 167 to 242, plates XI to XVI, deals with the leucocytes. In the evolution of the neutrophil leucocyte Ferrata distinguishes between the 'proneutrophilic myeloblast' and the 'neutrophilic promyelocyte.' Excepting for the presence of fine azurophilic granules in a basophilic cytoplasm, the former resembles the hemocytoblast in structure. In the neutrophilic promyelocyte the fine azurophilic granules are gradually replaced by neutrophil granules lying in an oxyphilic cytoplasm and the nucleus gradually assumes the coarser structure which is characteristic of the myelocyte. The proeosinophilic myeloblast contains very coarse azurophil granules and the eosinophilic promyelocyte eosinophil granules in addition. It should be pointed out here that most authors do not agree with Ferrata's assumption of

relationship between the character of the azurophil granulation and the further differentiation of the myeloblast, although it is generally conceded that the azurophil granulation of 'myeloid' cells differs from that of lymphocytes.

Part IV, forty-four pages and one plate, deals with the blood-platelets. Naturally a large portion of this chapter is devoted to the various theories on the origin of blood-platelets and to discussion of the extensive literature on the subject. The discussion is unusually complete for a book of this kind.

Ferrata derives blood-platelets from megakaryocytes, as originally discovered by Wright, and also from 'monocytoid' cells having azurophil granules arranged in small groups as in blood-platelets. These latter cells are found especially in the bone-marrow of the embryo.

Part V, pages 313 to 399, dealing with the hematopoietic tissues, is the most interesting and original section of the book. Due consideration of the connective tissue as a diffuse hematopoietic tissue is a decided and much-needed innovation. The 'hemohistioblast' (resting wandering cell of Maximow, clasmatoocyte of Ranvier) of the connective tissue and the 'hemocytoblast' comprise a uniform anatomical system, identical in embryological origin and differential potentialities; they form the hematopoietic parenchyme in the widest sense of the word.

The specific hematopoietic tissues of the bone-marrow, lymph nodes, and spleen are discussed first, this portion of the chapter being altogether too brief in proportion to the space devoted to the diffuse hematopoietic tissue. The hemocytoblast, similar in structure to Pappenheim's lymphoidocyte, is the progenitor of all the bone-marrow cells, and a similar cell in 'lymphoblastic function' gives rise to the lymphocytes of lymph nodes and spleen. The monophyletic theory is, therefore, accepted by Ferrata, but not the extreme unitarianism of Weidenreich and Maximow, for Ferrata believes in functional dualism to the extent that fully differentiated lymphocytes are incapable of differentiating into granulocytes or erythrocytes. In the spleen pulp the myeloid function of the hemocytoblast is retained to a certain extent, which explains the limited production of myeloid cells in the pulp of the normal adult.

The section devoted to the 'hemohistioblastic,' or 'diffuse hematopoietic' (connective) tissue is of special interest. The colloidal dyes (Trypanblau, Pyrrholblau, Lithiumcarmine) are made use of for the purpose of determining the relationships of the cells of this tissue. The primitive cell of this tissue is the resting wandering cell (Maximow) derived from an amoeboid embryonic mesenchyme cell and giving rise to all the other types of cells of the connective tissue. These are divided into chromophobe (without dye granules) and chromophile (with dye granules) types. The latter include the resting wandering cells, fat cells, endothelial cells, and fibroblasts. The fibroblasts, on account of the character of their dye granules, are regarded as highly differentiated cells, while fat cells and endothelial cells are considered to be functional adaptations of the hemohistioblast (resting wandering cell). The chromophobe cells include plasma cells, mast cells, eosino-

phils, and lymphocytes, and they are also differentiated from the hemohistioblast which loses its capacity for storing colloidal dyes during their differentiation.

In the opinion of the reviewer, much remains to be proved before this classification of Ferrata's can be adopted. The whole structure is built up on the assumption that the reaction of the cells to the colloidal dyes is specific. Recent work of the reviewer¹ seems to indicate that the reaction is not specific, but that the behavior of cells toward colloidal dyes depends entirely on functional and environmental conditions. In other words, the presence or absence of dye granules is not sufficient to enable us to distinguish between hemohistioblasts and lymphocytes, or between monocytes of the tissues and large mononuclears of the blood.

Serious objection may also be offered to the view that the 'hemohistioblast' is always a more primitive cell than the lymphocyte, and that the lymphocyte (of normal circulating blood) is a differentiated mature cell incapable of being transformed to a granulocyte and incapable of reverting to a hemohistioblastic resting wandering cell. In this connection it is sufficient to refer to the recent work of Weill,² who has shown conclusively that lymphocytes, even those having the structure of small lymphocytes, are capable of differentiation into granulocytes. It is true that these observations were made on human and mammalian thymus, spleen, and mucosa of digestive tract, but until real or even functional differences between lymphocytes of the blood and those of the tissues have been demonstrated, they must be regarded as valid objections to Ferrata's theory.

Numerous objections to Ferrata's view of the relationship between resting wandering cells and lymphocytes could be offered, but this is not the place for the lengthy discussion which would be necessary. Many of these topics are considered again in the following section, where the literature is given due consideration.

Part VI, pages 400 to 460, deals with the morphogenesis of the cells of the blood. The first part of the section is concerned with the genesis of the blood-cells of the embryo. Various theories are considered, but emphasis is placed on the results of the author's own researches. Although space will not permit discussion of this chapter, the reviewer wishes to call special attention to Ferrata's own conclusions in regard to the relationship of the blood-cells. The first basophilic lymphoid blood-cells derived from the mesenchyme of the early embryo are not lymphocytes, but a special type of 'primitive transitory hemocyto-

¹ DOWNEY, HAL 1917 Reactions of blood- and tissue-cells to acid colloidal dyes under experimental conditions. *Anat. Rec.*, vol. 12.

1918 Further studies on the reactions of blood- and tissue-cells to acid colloidal dyes. *Anat. Rec.*, vol. 15.

² WEILL, P. 1919 Ueber die Bildung von granulierten Leukozyten im Karzinomgewebe. *Virchows Archiv*, Bd. 226, Heft 2.

1919 Ueber die leucocytaeren Elemente der Darmschleimhaut der Säugetiere. *Arch. f. mikr. Anat.*, Bd. 93, Heft 1.

1919 Ueber das regelmässige Vorkommen von Myelocyten in der Milz des erwachsenen Menschen. *Arch. f. mikr. Anat.*, Bd. 93, Heft 1.

blasts' which are all under erythroplastic function. For a time they all differentiate into pronegaloblasts, megaloblasts, and megalocytes, the primitive red-cell generation of the early embryo. In the second phase, that of the hematopoietic activity of the liver, the mesenchyme cell (hemohistioblast) differentiates into a new type of primitive cell, the definitive hemocytoblast in myeloid function which in turn differentiates into erythrocytes, granulocytes, and megakaryocytes. This second hemocytoblast corresponds morphologically to the 'myeloblast' or stem-cell of the adult. In the third (fetal) phase, during which the lymphoid tissue appears, the mesenchymatous hemohistioblast gives rise to a hemocytoblast of lymphoid function which produces lymphocytes, although it is morphologically identical with the myeloid hemocytoblast. The different end-products are due to temporary functional differences only.

According to this scheme all the blood-cells are traced back to the fixed tissue cell, the hemohistioblast, the cell which stores colloidal dyes in the connective tissue of the adult. In the early embryo this cell differentiates into the primitive transitory hemocytoblast, and this in turn to the primitive red cells of the embryo (megalocytes), while in the adult, lymphoid and myeloid hemocytoblasts (functional differences only!) and monocytes are the products of its differentiation. The monocytes may also be derived from both the lymphoid and myeloid hemocytoblasts.

This scheme seems to harmonize the actual observed facts with both the unitarian and dualistic theories better than any other scheme which has been presented. A good part of this section of the book is devoted to discussion of the unitarian and dualistic theories and the last fifteen pages to the doctrine of Ferrata.

In part VII, pages 469 to 482, the author discusses the morphological significance of the cells of the blood and the hematological formula. The discussion of the significance of azurophil granulation is of special interest. Ferrata takes the stand that the presence of azurophil granulation in a myeloblastic lymphoid cell indicates beginning differentiation toward a granulocyte, which may be either an eosinophil or neutrophil granulocyte, according to the character of the azure granules. The azure granules are not transformed into the specific granules of the leucocytes, but are replaced by the latter. The presence of azurophil granulation in myeloid cells, therefore, indicates maturity and beginning differentiation and is of greater significance than the mere temporary secretory activity assumed by Pappenheim.

The reviewer has picked out only a few of the interesting and significant parts of the book for special mention. In closing he wishes to state that the book constitutes one of the most important recent additions to hematological literature. The statement on the title page that it is a "*Trattato per medici e studenti*" is somewhat misleading, for it is more than an ordinary text-book.

HAL DOWNEY,
University of Minnesota.

Resumen por el autor, J. A. Pires De Lima, Instituto de Anatomía
de la Facultad de Medicina,
Oporto, Portugal.

Estudio de un feto cíclope de cabra, macho, procedente de Nova
Goa (India Portuguesa).

El feto estudiado tenía un solo globo ocular con dos córneas y tres párpados, uno superior y dos inferiores. Ausencia completa de aparato nasal; labio superior terminado en punta roma y mandíbula prognata y recurvada hacia arriba. Cerebro chato y cráneo en gran parte lleno de un líquido seroso que se veía por transparencia a través del frontal. Ausencia de nervios olfativos y oculo-motores externos; un solo nervio óptico. Un solo frontal, dos parietales, dos inter-parietales, un solo maxilar y, por encima de él un hueso al cual llama el autor interzigomático. Una sola órbita. Agenesia del etmoides, de los cornetes, intermaxilares, palatinos, lacrimales, nasales y vómer. Tres de los incisivos ya en franca erupción. Se trata de un ciclocefaliano ciclocéfalo, según la clasificación de G. Saint Hilaire, y de un Cyclops arrhynchus según la nomenclatura de Gurlt. Se compara este caso con otros descritos por el mismo autor y por diversos teratologistas.

Translation by José F. Nonidez
Cornell University Medical College, N. Y.

ANATOMY OF A FETUS OF A CYCLOPEAN GOAT

J. A. PIRES DE LIMA

Institute of Anatomy of the Faculty of Medicine of Oporto (Portugal)

SIX FIGURES

Prof. Froilano de Melo, of the School of Medicine and Surgery of Nova Goa (Portuguese India), sent me for study a monstrous fetus of a goat. It was received by the Museum on the 4th of January, 1919, immersed in alcohol.

The skin was covered with white hair, except at the upper part of the head, where there was an extensive area of black hair, stretching forward and encircling the eyelids, as well as the lips; besides, some small disseminated black spots. At the top of the head there were noticed three vortices of hair arranged in the form of a triangle.

The fetus was of the male sex, and kept the umbilical stump of the cord. Only the head was abnormal. On external inspection (fig. 1), the presence of a single median eye was noted, under which there was found a deep depression corresponding to the nasal apparatus, which was completely missing. The tongue protruded from the mouth and inclined to the left. Above it, in the median line, one noted the upper lip ending in a blunt point, and underneath, a voluminous mandible, prognatic and turned up.

The ocular globe of this monster was possessed of two corneae separated by a narrow light median zone. It was surrounded with three eyelids, an upper one with a free and convex border and two lower eyelids convex free at the borders and united in the median line. Only one conjunctiva connected the ocular globe to the deep faces of the three eyelids, in its reflexion forming conjunctival culs-de-sac, superior, inferior, and lateral, right and left. The palpebral cleft was 2 cm. wide and 1 cm. high.

Close to the corners of the eye there were found long lashes, and on the right one there were observed long hairs inserted above and below the eyelids. In the depression existing between the eye and the mouth, on the wrinkled skin, two vortices of hair on the median line were to be seen and two tufts of hair (tentacles) crowned the anterior part of the lips.

The head was flattened transversely. The following measurements were obtained:

	<i>cm.</i>
Maximum anteroposterior diameter.....	5
Maximum transverse diameter.....	4
Distance from the nape to the symphysis of the mentum.....	7.3
Length of each ear.....	5

The cephalic index 80.¹

The remainder of the fetus presented the following measurements:

	<i>cm.</i>
Circumference of the neck.....	9
Length from the nape to the basis of the tail.....	25
Length of the tail.....	4
Perimeter behind the implantation of the thoracic members.....	22

This specimen did not possess behind the mandible the pyriform appendices called in Portuguese brinco (ear-rings), commonly seen in goats, representing an auditory appendage of the second branchial cleft.² After having studied the external morphology, the osseous skeleton was exposed. The upper surface of the skull (fig. 2) presents the form of a lozenge, to the angles of which the frontal, parietal, and occipital bones, respectively, correspond. The cranial vault presented a smooth surface, comprising the following bones: frontal (*F*) single; parietal (*P*, *P*) separated by the sutura interparietalis; squama occipitalis (*SO*); two interparietal bones (*IP*), and finally a rhombic Wormian

¹ According to Chauveau and Arloing (*Traité d'Anatomie comparée des animaux domestiques*, 5e éd., Paris, 1903), the cephalic index of the caprid family should vary between 55 and 63.

² Louis Blanc—Les pendeloques et le canal de Soyer (*Journal de l'Anatomie et de la Physiologie*, 1897).

J. A. Pires de Lima—Agenesia do Canal auditivo externo e atrofia da orelha (Anais Científicos da Faculdade de Medicina do Porto, vol. 2, no. 3, 1915).

bone (*W*), between the frontal and the parietal bones. All these bones were connected by well-defined sutures. On the superior part of the frontal bone there was found in the median line the



beginning of metopic suture. Below it one noticed a slight roundish protuberance, behind which and below a transverse depression was to be found (fig. 3, *d*). Perhaps this protuber-

ance represented the first stage of a pin for the implantation of a future horn.³

On the lateral face (fig. 3) were to be seen: the squama occipitalis (*S O*), the interparietal (*I P*), the parietal (*P*), the frontal (*F*), the squamosal (*S*), the mandibular (*m*), the maxillary (*M*), the zygomatic (*Z*) bones, and moreover, one which I call interzygomatic, and was to be found between the two zygomatic bones, stretching to the median part of the orbital floor (figs. 3 and 4, *Iz*).

As not the slightest vestiges of the nasal fossae were to be found, there was also complete absence of the following bones: ethmoid, turbinated, intermaxillary, palatine, lacrymal, nasal, and vomer. The incomplete ossification of the bones of the base of the skull did not permit me to study the sphenoid, occipital, auricular part of the temporal, as well as the pterygoid. The alveolar portion of the maxillary bones was still also cartilaginous.

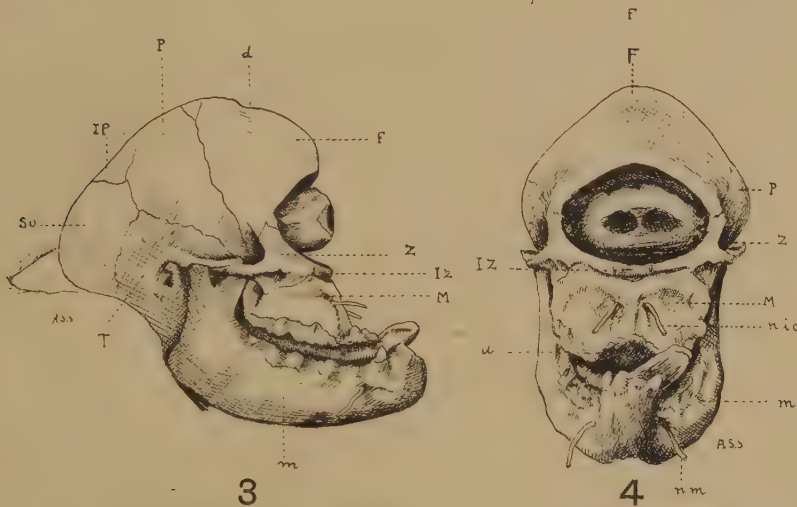
In figure 4 one observes the aspect of the skeleton of the head, seen from in front. One did not note any median sutures separating the maxillary bone and the symphysis of the mandibula was about changing into synostosis.

The median and inferior parts of the single maxillary bone, not yet ossified, terminated in a reversed point (fig. 4, *a*). It was above this cartilaginous prolongation that the upper lip ending in a beak was to be found. Between the two zygomatic bones there was a median rectangular osseous segment, which I have termed the interzygomatic. The mandible (figs. 3 and 4, *m*), as we have seen, is extensive and protruding. On both sides of it the mentales nerves (*n m*) take exit. From the maxillary bone, close to the median line, the infra-orbital nerves (*n i o*) emerged. The orbit was ovoid in form and of median position, 25 mm. broad and 19 mm. high. The distance from the inferior border of the orbit (median line) to the part of the median prolongation of the maxillary bone was 15 mm.

³ Plutarch says that a sheep with a single horn, very strong and solid in the middle of the front, was once brought to Pericles. Anaxagoras should have dissected the head of the animal and seen that its brain was pointed like an egg and its more pointed pole was in connection with the root of the horn.

The vault of the orbit was formed by the frontal bone, the lateral walls by the zygomatic bones and the floor, the ossification of which was incomplete, appeared to be formed by the zygomatic, interzygomatic, and perhaps the maxillary bones.

On removing the skull-cap, the brain was found to be reduced to a shapeless lamina of nervous tissue. The cerebellum appeared to be normal. The greater part of the cranial cavity, within the wide space, comprised between the dura mater and the upper face of the brain, reduced and flattened, was filled by fluid.



Concerning the cranial nerves, the following may be recorded: Of the olfactory nerves not the slightest vestiges were to be found; there was a single optic nerve, fasciculate, and in the median line (fig. 5, *II*); next in order the III, IV and V pair; the patheticus was thicker than the common oculomotor; there were no traces of the external oculomotor; the auditory formed a single fascicle on either side (*VII*, *VIII*); behind and within another fascicle represented the glossopharyngeal, the pneumogastric, and the spinal nerves (*IX*, *XI*) and a little behind and within that fascicle lay the great hypoglossal nerve.

After the dura mater had been taken away from the base of the skull, this presented the appearance reproduced in figure 6.

One notices in it from before to behind: the single optic nerve, on the median line, penetrating an optic foramen (*II*) as wide as the occipital one; a nerve (*III, IV*), which must represent the common oculomotorius and the pathetic nerve, distinct before the dura mater had been withdrawn; the n. trigeminus (*V*); the facial and auditory nerves (*VII, VIII*), and last all the following ones (*IX- . . .*) in a single fascicle. The hypoglossal nerve, which appeared well detached before the removal of the dura mater was not to be seen afterward.

The ocular globe was large, oval with a single optic nerve and a single cavity. Only the cornea showed signs of duplicity in the forepart. On opening the ocular globe, this was found so macerated as to make it unsuitable for study.

Contrary to what is generally the case, in this specimen,⁴ which I suppose to be a dead-born fetus, three of the incisor teeth had already appeared: the pincer, the first right mitoyenne, single, as well as the first left mitoyenne, this being considerably developed. The left pincer and the second mitoyennes were beginning to appear.

The dissection of the neck and the autopsy of the thorax and of the abdomen did not reveal any abnormal disposition worth registering.

According to the classification of I. Geoffroy Saint-Hilaire,⁵ this monster belongs to the class of the Cyclocephaleans; that is to say, to the class of monsters having the nasal apparatus more or less completely atrophied, the apparatus of vision imperfectly formed, sometimes quite rudimentary, directed to the median line and almost always united.

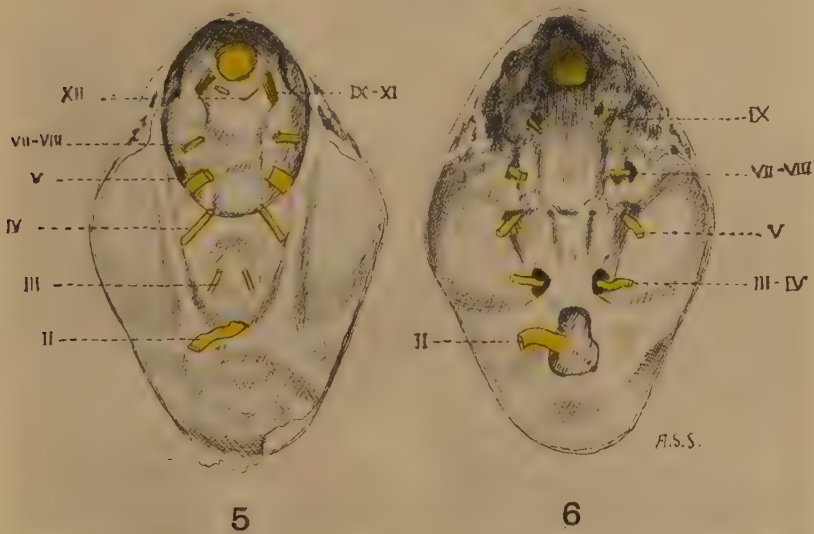
It still belongs to the 'Cyclocephalus' genus, to the cyclocephaleans having a single orbital cavity, two contiguous eyes or a double eye occupying the median line, the nasal apparatus atrophied and no proboscis.

⁴ Chauveau and Arloing (loc. cit.) say that the pincers appear from the third to the fifth day, as well as the first mitoyenne. The second mitoyennes would make their appearance about the tenth day after birth.

⁵ I. Geoffroy Saint-Hilaire *Histoire Générale et particulière des anomalies d'organisation chez l'Homme et les animaux*, Paris, 1836.

According to Gurlt's⁶ classification, my specimen should be classified as a 'Cyclops arrynchus.'

Besides this cyclops, I have already had an opportunity to study three in the human species.⁷ A fetus ♀ Cyclocephalean rhyncephalus, having an ocular globe adherent to the eyelids (1 superior and 2 inferior) without conjunctival culs-de-sac, either superior or inferior. The ocular globe, shapeless, seemed to be formed by two eyes which had fused into one. There were two frontal bones with sutura metopica.



The second case was a Cyclocephalean cyclocephalus ♂. A superior eyelid and an inferior one, formed, by two soldered palpebrae. Ocular globe atrophied and deformed. Frontal single. Genu varum.

The third case was a skull of a fetus with a median orbit, a single optic foramen, frontal single, very salient frontal and parietal protuberances.

⁶ Taruffi-Storia della Teratologia, T. 6, Bologna, 1891.

⁷ J. A. Pires de Lima, Sobre tres monstros ciclocefalios (Anais Scientificos da Faculdade de Medicina do Porto, vol. 4, no. 2).

In an Otocephalean pig ♀ which I studied,⁸ the frontal and parietal bones were reduced to a single piece, forming the cranial vault.

An Opodymus cat ♂, which I described,⁹ had a concentric orbit with a double eye, apparently rather similar to the single ocular globe of the present observation. However, it has two optic nerves, besides two corneae.

According to Geoffroy Saint-Hilaire,¹⁰ the Cyclocephalean rhinocephali, as in the present observation, mostly have too small an encephalon to fill the cranial cavity; there exists then almost always a larger or smaller quantity of fluid,

In 1860, Gintrac¹¹ studied a human fetus ♀ born at term, Cyclocephalean rhinocephalus. Its skull was much reduced. The median eye had two corneae and the hind part of the skull a sac full with a lemon-yellow fluid. The brain was atrophied. The olfactory nerve was missing; perhaps also the patheticus, the optic nerves were in close proximity.

Taruffi¹² also mentions the presence of a remarkable quantity of liquid within the skull of the cyclops. The same author records that in these monsters the olfactory nerves are always missing and that there is a single optic nerve with the chiasma absent.

Taruffi, moreover, states that the cyclopia is much more common in the female sex.

Phisalix¹³ has studied four monsters cyclocephalean or otocephalean, one in dog, two in sheep, and a human fetus; in the last, attention was immediately drawn by the absence of cerebral hemispheres normally constituted; the skull once opened, there came out a serous, light, opaline liquid, lodged in a sac, at the

⁸ J. A. Pires de Lima, Étude d'un monstre otocéphalien (Bulletin de la Société Portugaise des Sciences Naturelles, T. 8).

⁹ J. A. Pires de Lima, Study of an opodymus kitten (Journal of Anatomy, vol. 52).

¹⁰ I. G. Saint-Hilaire, loc. cit.

¹¹ Gintrac, Considérations sur la cyclocéphalie (Actes de l'Académie Impériale de Sciences, Belles lettres et Arts, Bordeaux, 1860).

¹² Taruffi, loc. cit., T. 8, Bologna, 1894.

¹³ Phisalix, Monstres cyclopes (Journal de l'Anatomie et de la Physiologie, Paris, 1889).

bottom of which was the encephalon. Instead of brain, one noted a whitish and flattened mass. In this specimen nerves of the I and IV pair were wanting.

Rabaud,¹⁴ in an extensive memoir, has discussed fifty abnormal chicken embryos, concluding, in accordance with Dareste's opinion, that the cyclocephalia is due to a developmental disturbance of the encephalon.

Watkyn-Thomas¹⁵ has described a human fetus ♀ with incipient cyclopia; it had two eyes drawn nearer and a single nasal orifice, without olfactory nerves. In the Museum of the Anatomical Institute I have stored a similar monster, which I will presently study.

Lately in America several works dealing with cyclopia have been published. I shall mention the following:

Stockard¹⁶ has made some interesting experiments on teratogeny of fishes, artificially obtaining cyclopean monsters by means of solutions of $MgCl_2$ or $Mg(NO_3)_2$ and he believes it may be concluded that such monstrosities in man and other mammals are due to an excess of magnesium salts in the maternal blood or in the amniotic fluid.

Warren Lewis¹⁷ has likewise published experimental observations on teratogeny of fish embryos.

Whitehead¹⁸ has studied a human fetus cyclocephalus.

Chidester¹⁹ has described a cyclopean rat, an atocephalean pig, as well as the brain of a human fetus cyclocephalean. The same author²⁰ has studied some double monstrosities in fishes, one of them complicated with cyclopia.

Finally, Werber²¹ has also occupied himself with experimental teratology and specially with teratophthalmia.

¹⁴ Rabaud—Recherches embryologiques sur les cyclocephaliens (idem, 1901-02).

¹⁵ Watkyn, Thomas, A cyclopean foetus with hernia encephali (Journal of Anatomy and Physiology, vol. 44).

¹⁶ Charles Stockard, The artificial production of one-eyed monsters and other defects, which occur in nature, by use of chemicals (Anat. Rec., vol. 3).

¹⁷ Warren Lewis, The experimental production of cyclopia in the fish embryo (*Fundulus heteroclitus*) (idem).

¹⁸ Whitehead, A case of cyclopia (idem).

¹⁹ Chidester, Cyclopia in mammals (The Anatomical Record, vol. 8).

²⁰ Idem, Twins in fish, one with cyclopean deformity (idem).

²¹ Werber, Experimental studies aiming at the control of defective and monstrous development (idem, vol. 9).

Resumen por el autor, O. F. Kampmeier,
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Los cambios en el plan sistémico venoso durante el desarrollo y
la relación de los corazones linfáticos de los
anuros con estos cambios.

Después de indicar brevemente los trabajos de Goette y Hochstetter sobre el desarrollo del sistema venoso en los anfibios, el autor describe la formación de las venas sistémicas en Bufo. Mediante esquemas demuestra que existe una correspondencia mas estrecha en la disposición primaria y cambios de estas venas en los vertebrados inferiores y superiores, que lo que se ha supuesto. Por ejemplo, el componente subcardinal del sistema venoso existe ya en los estados jóvenes de embriones de anuros. El autor demuestra también como se producen las diferencias, aparentemente irreconciliables, entre la situación de las comunicaciones linfático-venosas del embrión y las de los individuos completamente desarrollados. En el anfibio anuro adulto, por ejemplo, los corazones linfáticos anteriores desembocan en la correspondiente vena vertebral anterior, que a su vez es trigutaria mas anteriormente de la vena yugular interna. En el embrión, por otra parte, el corazón linfático anterior, que se origina a expensas de la vena de la linea lateral que pasa a este nivel, comunica con el seno venoso pronefrótico, que representa la confluencia de las venas pre- y postcardinales alrededor del pronefros. De un modo semejante, los corazones linfáticos posteriores se originan a lo largo de las venas de la linea lateral, pero en el adulto vienen a ponerse en relación con las venas isquiáticas por intermedio de las venas vertebrales posteriores. Los esquemas demuestran además con que facilidad las variaciones tan comunes se producen por la expansión, reducción o persistencia de diferentes segmentos de las venas intersegmentarias originariamente simétricas, cuyas variaciones dan lugar a diferentes relaciones con los troncos venosos principales.

Translation by José F. Nonidez
Cornell University Medical College, N. Y.

THE CHANGES OF THE SYSTEMIC VENOUS PLAN DURING DEVELOPMENT AND THE RELATION OF THE LYMPH HEARTS TO THEM IN ANURA¹

OTTO F. KAMPMEIER

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NINE FIGURES

Our knowledge of the primary venous plan of anuran embryos and its subsequent transformation is based almost wholly on the observations of Goette and Hochstetter.² In his classic work, "Entwicklungsgeschichte der Unke" (1875), Goette gives a clear account of the development of the systemic veins of Bombinator. In some respects, however, the venous system of Bombinator differs from that of the more typical Anura, the most marked difference being the persistence normally of the anterior portions of the postcardinal veins, for which the term 'venae azygae' has generally been employed in the literature. In the retention of the postcardinals alongside of a postcava, Bombinator closely resembles the urodeles, the salamander, for example. Hochstetter ("Beiträge zur vergleichenden Anatomie und Entwicklungs-

¹ This paper represents a section of a larger paper on the origin and development of the lymphatic system in Anura which was originally intended for publication in a monograph, as indicated in The Anatomical Record, vol. 16, August, 1919. Adequate funds were not available to publish that work as such, and it was decided to split it into several parts and have them appear as separate papers in two or three of the anatomical and morphological journals. Though, in a sense, the unity of the work is thereby destroyed, the disadvantage is offset by the advantage of its wider circulation.

² For a comprehensive list of the literature on various aspects of the venous system of the Anura, I refer to the following works: "Beiträge zur vergleichenden Anatomie und Entwicklungsgeschichte des Venensystems der Amphibien und Fische," by Hochstetter in Morphol. Jahrbuch, 1888; "Anatomie des Frosches," by Ecker and Wiedersheim, 1896 (Gaupp's revision); 'Vergleichende Anatomie der Wirbeltiere,' (7th ed., 1909), by Wiedersheim.

geschichte des Venensystems der Amphibien und Fische," *Morphol. Jahrbuch*, 1888) has indicated wherein the differentiation of the cardinal system of veins in the frog varies from that in *Bombinator*.

Since the time of Goette's and Hochstetter's work, no systematic study, so far as the writer is aware, has dealt with the above problem in the light of the more recent work on other vertebrates, nor have the changing relations of the larger venous branches to the main trunks during development been considered. The following diagrams and brief description show that a closer correspondence exists between the lower and the higher vertebrates in the genetic history of their venous systems than has been supposed.

A matter of greater importance in the writer's opinion, is the fact that no account has demonstrated how the seemingly irreconcilable differences between the situations of the lymphatico-venous communications of the embryo and those of fully formed individuals are brought about. This process has interested the writer greatly not only in his investigation of the lymphatic system of *Anura*, but also in his effort to furnish a systematic presentation of the comparative morphology of the systemic lymphatics in vertebrates.³ It is a well-established fact that in the adult anuran amphibian the anterior lymph hearts discharge into the corresponding anterior vertebral vein, which further cephalad is a tributary of the internal jugular vein. In the embryo, on the other hand, the anterior lymph heart, arising on the transient vein of the lateral line, communicates with the pronephric venous sinus, which represents the confluence of the pre- and postcardinal veins around the pronephros and is continued to the sinus venosus as the duct of Cuvier. Similarly, the posterior lymph hearts arise along the lateral-line veins, but in the mature form come in relation to the ischiadic veins through the posterior vertebral veins. In comparing the anterior lymphatic taps of an adult anuran with those of a mammal, for example, one would hardly conclude that they are identical, and yet, when their embryonic history is revealed, both can be definitely re-

³ This work is in process of preparation.

ferred to the cardino-Cuvierian district, where such communications occur with remarkable constancy either temporarily or permanently throughout the entire series of vertebrates, from the lowest to the highest. In the same way, the posterior lymph hearts can be compared with certain members of the lateral series of intersegmental lymph hearts in the tailed amphibians on the one hand and with the iliac and coccygeal lymph hearts of reptiles and birds on the other. Studies like these have impressed the writer, as other investigators have doubtlessly been impressed before, that biological homology becomes an exact science only when it rests squarely on the comparative anatomy of the embryo.

The following account is based almost wholly on a study of the toad, *Bufo*. The younger embryonic stages belong to the European species, *Bufo vulgaris*, the later stages, including young individuals shortly after metamorphosis, to the American form, *Bufo lentiginosus*. Besides these, a few mature frogs, *Rana pipiens*, were examined. The inserted diagrams have been constructed from a series of graphic reconstructions of the venous system of progressively consecutive stages.

Toad embryos (*Bufo vulgaris*), 4 to 5 mm. long, possess the primary venous ground plan of vertebrate animals, namely, the simple symmetrical cardinal system, as illustrated in figure 1. There are a number of peculiarities; however, which should be emphasized, since they are directly or indirectly involved in the development of the lymph hearts and associated veins. At the junction of the precardinal (internal jugular) and postcardinal veins, a proportionately large venous sinus (*si. proneph.*) has been formed, a broad plexus of channels which encompass the tubules of the pronephros. Of greater interest are the intersegmental veins (*1-8 v. seg.*),⁴ a metameric series of vessels which pass ventrally between the myotomes and epidermis to empty

⁴ It should be stated that since there is a possibility of the reduction of intersegmental veins at the extreme anterior end of the series during phylogenesis, just as the spinal ganglion I is an evanescent structure, the designation of the intersegmental veins by specific numerals must be taken with reserve when homologizing *Bufo* with other Amphibia.

into the cardinal vein trunk, the first three into the pronephric sinus and the remainder into the postcardinal. But not all of them are present at the same time, for in their appearance, as with other events of embryogenesis, the processes of development proceed in an anterioposterior direction. When the foremost intersegmental veins have been established, the more caudal ones may still be lacking, and when these have been laid down and have attained importance, the anterior ones have already begun to disappear or become modified (figs. 1 to 4); only in the lower Amphibia do the intersegmental veins persist as such during the entire life of the animal. Occasionally, too, there are slight irregularities in their arrangement, such as the convergence of two consecutive vessels to join the postcardinal at the same point. But these are insignificant fluctuations, and in the diagrams they have been disregarded.

The original condition of the postcardinal, lying against the medial side of the primary excretory tube of Wolffian duct, is soon altered by the formation of a second channel on its lateral side as the result of longitudinal anastomoses between the intersegmental veins near their points of confluence with the postcardinal (figs. 2 and 3). At the same time, these two parallel channels, which for the time being may be considered as the medial and lateral divisions of the postcardinal (*med. and lat. v. card. post.*), become united by numerous transverse anastomoses which pass around, over, and under the Wolffian duct so that this structure becomes enclosed by a cylindrical venous plexus. Hochstetter states that the latter condition only obtains in the salamander, but the writer's material shows without doubt that such takes place normally in the larval Anura as well. At the posterior end of the trunk, the postcardinal vein fuses with its fellow of the opposite side and is prolonged into the tail as the caudal vein (*v. caud.*). Here, too, a paired vessel, the common rudiment of the proximal part of the abdominal and external iliac (*v. iliac.*) veins, branches off and passes laterally around the hind-gut to its under side where it extends forward a short distance.

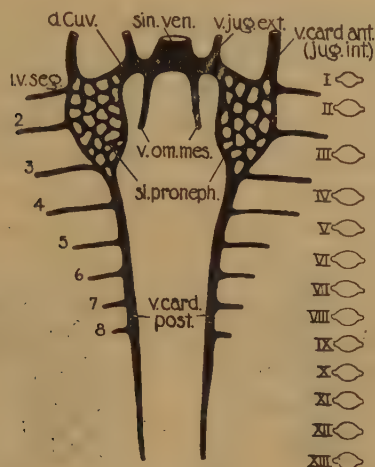


Figure 1

Figs. 1 to 4, diagrams of the systemic veins in 4-, 6-, 7-, and 10-mm. embryos of *Bufo vulgaris*, respectively; figs. 5 to 7, in 15- and 18-mm. tadpoles of *Bufo lentiginosus*, and a stage immediately before metamorphosis; fig. 8, in the young *Rana pipiens*. All figures (except 9), $\times 33\frac{1}{2}$. As all the structures are shown in the diagrams as lying in the same plane, there is, of course, a certain degree of distortion; thus, the intersegmental veins appear to be lateral tributaries of the cardinal veins when in reality they are dorsal ones. The spinal ganglia, I, II, III, etc., were introduced to indicate levels.

cor lym. ant., cor lymphaticum anterior

cor lym. post., cor lymphaticum posterior

d. Cuv., ductus Cuvieri

si. proneph., sinus pronephros

sin. ven., sinus venosus

v. abdom., vena abdominalis

v. brach., vena brachialis

v. card. ant., vena cardinalis anterior

v. card. post., vena cardinalis posterior
(*med.* and *lat.*), medial and lateral divisions

v. caud., vena caudalis

v. cav. ant., vena cava anterior

v. cav. post., vena cava posterior

v. cut. fem. post., vena cutanea femoris posterior

v. cut. mag., vena cutanea magna

v. dors. lumb., vena dorso-lumbalis

v. fem., vena femoralis

v. hep. rev., vena hepatica revehens

v. iliac., vena iliaca

v. iliac. trans., vena iliaca transversa

v. ischiad., vena ischiadica

v. Jacobs., vena Jacobsonii

v. jug. ext., vena jugularis externa

v. jug. int., vena jugularis interna

v. lat., vena lateralis

v. om. mes., vena omphalo-mesenterica
(vitelline veins)

v. ren. adv., vena renalis advehens

v. seg. 1, 2, 3, etc., venae intersegmentalis

v. subcard., vena subcardinalis

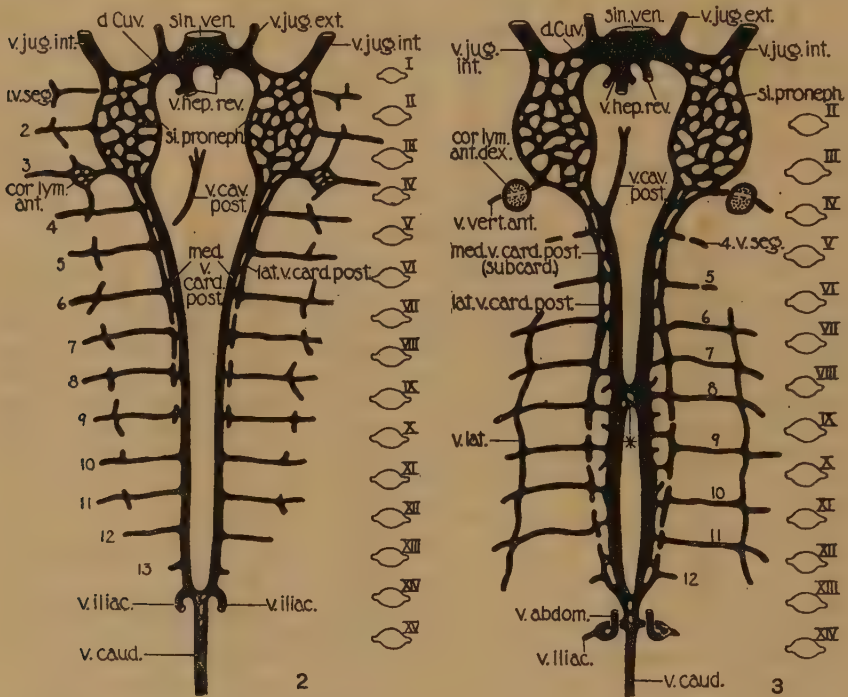
v. subclav., vena subclavia

v. vert. ant., vena vertebralis anterior

v. vert. post., vena vertebralis posterior

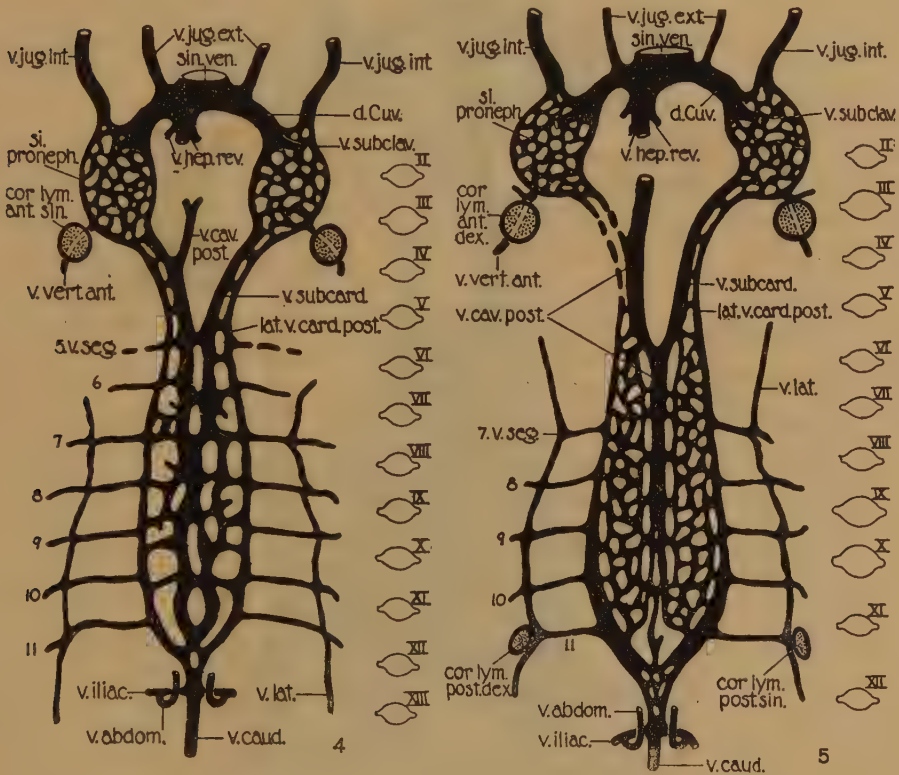
*, interanastomosis between the subcardinals

Soon after, in 7-mm. embryos, the two divisions of the post-cardinal begin to diverge from one another in the middle of their course (fig. 3) due to the crystallization, as it were, of the anlagen of the mesonephric tubules, which crowd between them. Consequently, the medial postcardinal components, which may now be termed the *subcardinal veins*, since they are unquestionably the homologues of vessels bearing the same name in higher verte-



brates, approach each other in the center, and the first hint of their eventual fusion to create the posterior half of the future postcava is offered by a simple interanastomosis (fig. 3,*) at the level of the eighth spinal ganglia. Coincident with the merging of the subcardinals (figs. 4 and 5) occurs the formation of the proximal half of the postcava; this is already potentially present in the right vitelline vein, which, at first equal in size to the left (fig. 1, *v. om. mes*), grows larger (figs. 2 to 5, *v. hep. rev.*), and,

traversing the liver, establishes continuity with an apparently independent segment which is developed between the liver and the right postcardinal (fig. 2). This segment soon becomes confluent with the latter vein at the level of the fourth spinal ganglia (fig. 3), and the postcaval trunk is complete. Obviously,



much of the blood in its return from the caudal regions of the body to the heart is now deflected through the postcava, and in time, as an increasingly greater volume of blood follows this more direct route, the portion of the original postcardinal veins between the postcava and the pronephric sinus of both sides gradually falls into disuse and atrophies, the right disappearing earlier than the left (figs. 5 to 7).

Changes as far-reaching as the above take place caudally. The most distal segment of the subcardinal (medial postcardinal division) does not fuse with its fellow, but undergoes reduction

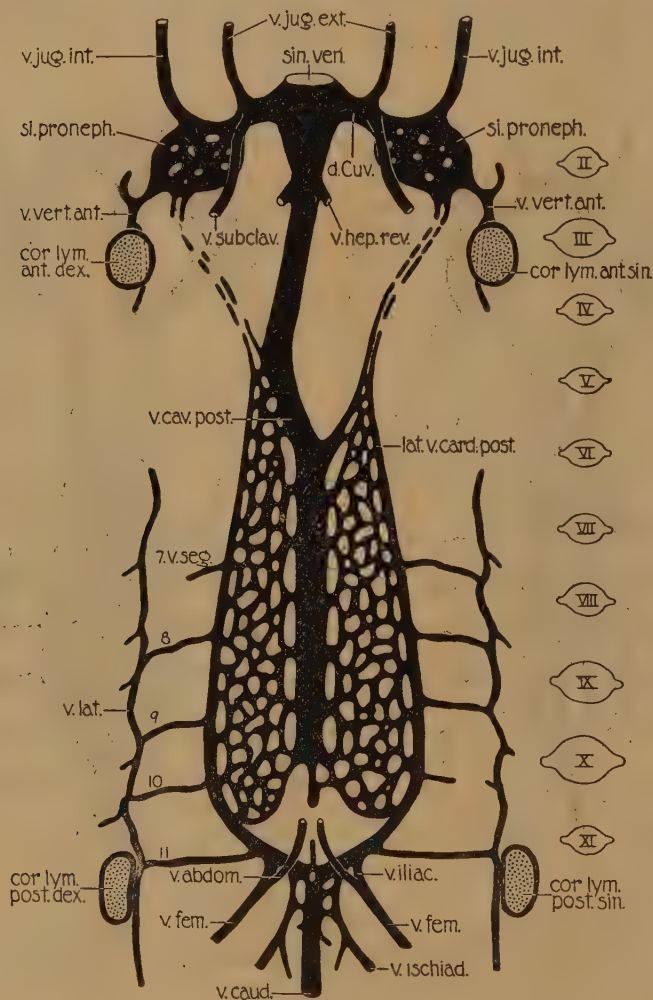


Figure 6

and finally breaks away (figs. 4 to 6), thus severing the connection between caudal vein and postcava. Hence, all of the blood from the hinder regions is compelled to flow through the expand-

ing lateral postcardinal divisions which may now be called the *venae renales advehentes* (Jacobsen's veins, figs. 7 and 8), thence through the sinusoids of the mesonephroi to enter the postcava

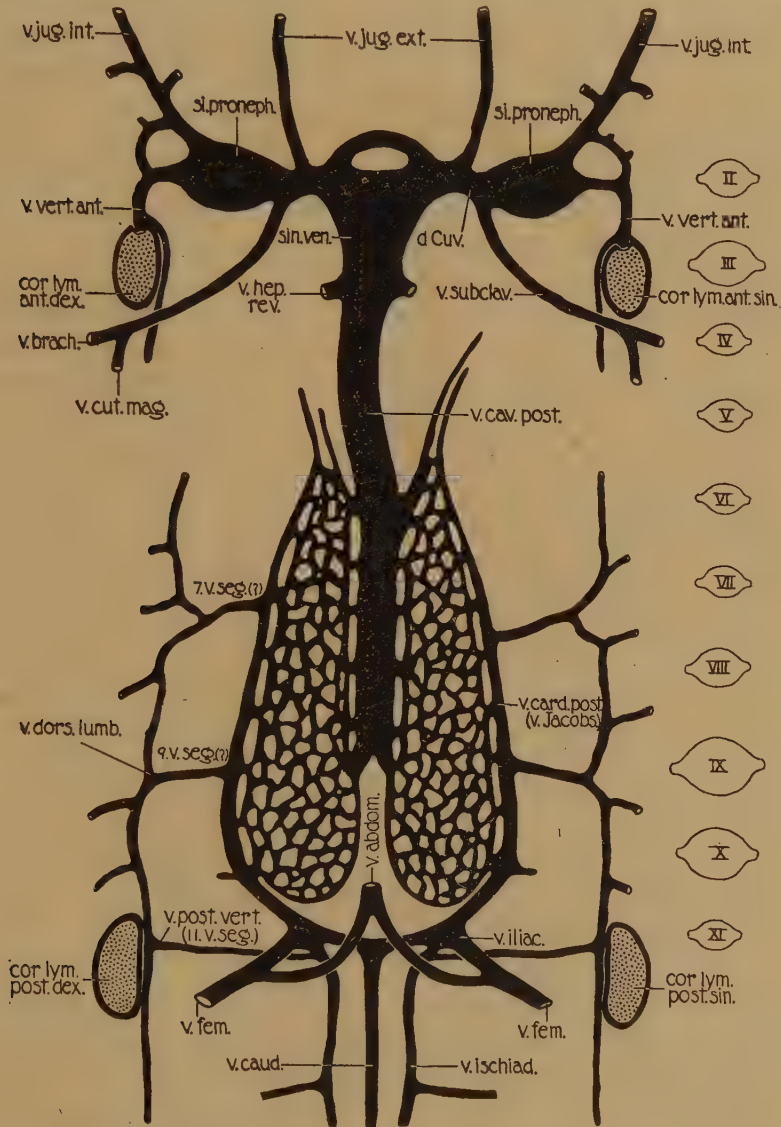


Figure 7

through the revehent branches. In the meantime, the paired abdominal vein has merged anteriorly into a single vessel which joins the hepatic portal vein (not shown in the diagrams) and so produces a second pathway of return for the blood-stream from the posterior region. Gradually, the two unfused and divergent rami of the abdominal vein remain united with the external iliac veins which extend out into the developing limb buds as the rudiments of the femoral veins. Extensions of the postcardinals backward along the caudal vein (fig. 6) represent the anlagen of the ischiadic veins (*v. ischiad.*) which enlarge as the hind extremities develop and the caudal vein degenerates. The transverse iliac veins (*v. iliac trans.*), obliquely connecting the external iliac and ischiadic veins, are a later acquisition (fig. 8).

As the mesonephroi are progressively differentiated and as they assume the function of urea excretion, the pronephroi suffer regression in a corresponding degree (figs. 7 and 8). During the growth of the tadpole a marked shifting of relations occurs, for, as the diagrams indicate, the pronephroi in earlier stages lie slightly back of the niveau of the sinus venosus and are directly placed in the path of the postcardinals, but later, owing to the atrophy of the proximal segment of these channels, they come to lie anteriorly, at the junction of the external and internal jugulars.⁵ In fact, the pronephric sinus at the time of metamorphosis forms the terminus of the internal jugular where it appears as a swelling (fig. 8), but the difference in diameter is gradually equalized by further reduction of the sinus. Changes like these are instrumental in bringing about the striking dissimilarities between the venous relations of the lymph hearts in embryonic and in adult stages. Further changes in this region that produce the definitive relations of the anterior lymph hearts to the veins are indicated in the following paragraph.

Associated with the alterations of the large venous trunks, radical modifications take place in the series of intersegmental veins. Another paper will show how the first three of these are intimately concerned in the development of certain lymph-

⁵ In using the term 'external jugular vein,' I am following Gruby and Ecker; Goette and many other authors refer to this vein as the 'inferior jugular.'

atic channels, the third contributing largely to the formation of the anterior lymph heart (fig. 2, *cor lym. ant.*). Only the mouth of the anterior vertebral vein (*v. vert. ant.*) of later stages, in

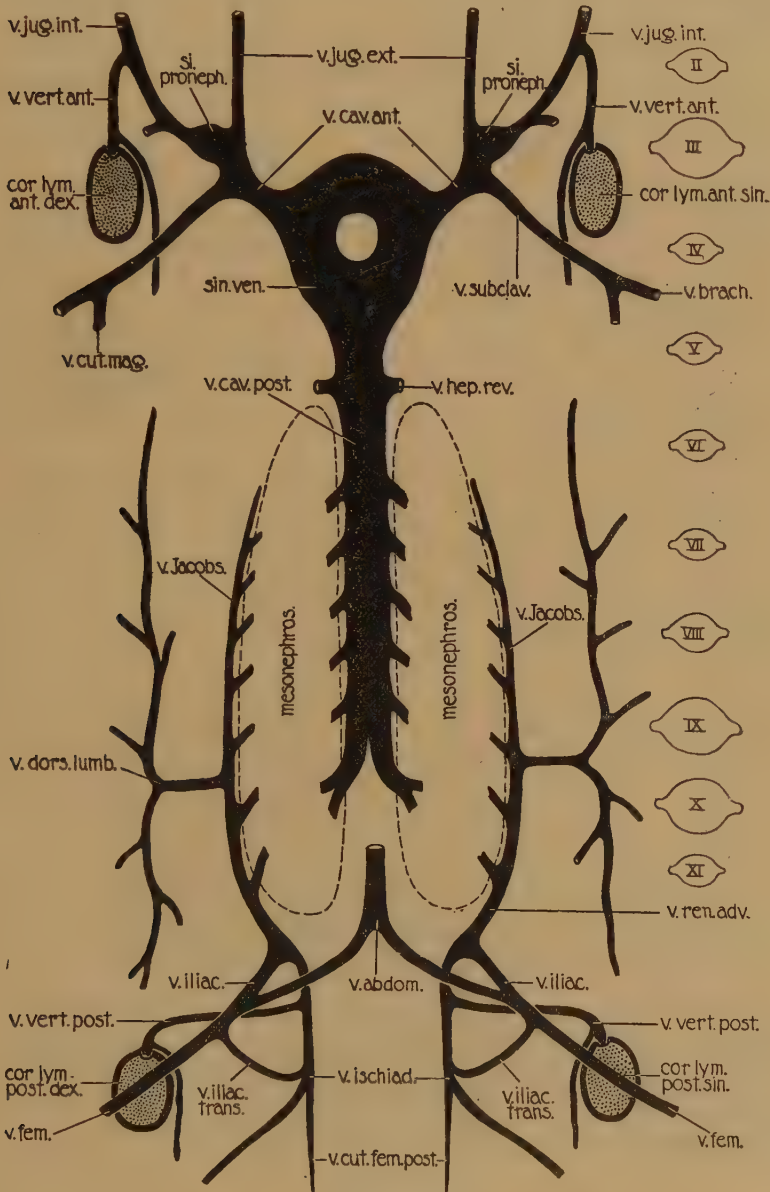


Figure 8

other words, the efferent channel of the anterior lymph heart, can be considered as a direct transformation or derivative of the proximal portion of the third intersegmental vein, the remainder being an outgrowth from the latter just medial to the lymph-heart anlage. During the period of the degeneration of the anterior segments of the postcardinals and the consequent dwindling of the pronephric sinuses, each anterior vertebral vein, besides extending at first in a posterior direction, soon develops a second fork which extends forward and eventually establishes a connection with the internal jugular some distance anterior to the pronephric sinus. Sometime later, the original connection of the anterior vertebral vein with the vestige of the pronephric sinus, now the terminal portion of the internal jugular, breaks away, and the secondary junction farther cephalad becomes the permanent outlet of the lymph stream from the anterior lymph hearts. These changes are clearly expressed in the diagrams 5 to 8, inclusive.

During development all of the intersegmental veins back of the anterior lymph hearts become interjoined by a longitudinal anastomosis (figs. 2 and 3) which may be termed the lateral vein (*v. lat.*) because it courses in the lateral-line region and is without doubt homologous with a similar vein in the tailed amphibians. Subsequently, the termini of all intersegmentals except the 9th and 11th (fig. 7) in toad embryos become very much reduced or vanish, although variations happen, such as the persistence of the vessels in intervals other than those. The anterior one of the retained intersegmentals becomes the transverse piece or mouth of the dorsolumbar vein (figs. 7 and 8, *v. dors. lumb.*), while the greater extent of the lateral vein becomes its longitudinal portion (rami iliolumbalis and iliacus). While these changes are taking place, the posterior lymph heart (*cor. lym. post.*) on each side⁶ develops from a lymphatic plexus along

⁶ *Bufo* possesses only one posterior lymph heart on each side. Among the frogs there are multiple posterior lymph hearts, from two to four in number on each side in the adults; thus in the American common species, *Rana pipiens*, there are normally two pairs of these (diagram 9) with the occasional vestige of a third, present in the tadpole. The development of these hearts and their relation to the veins will be considered in one of the subsequent papers.

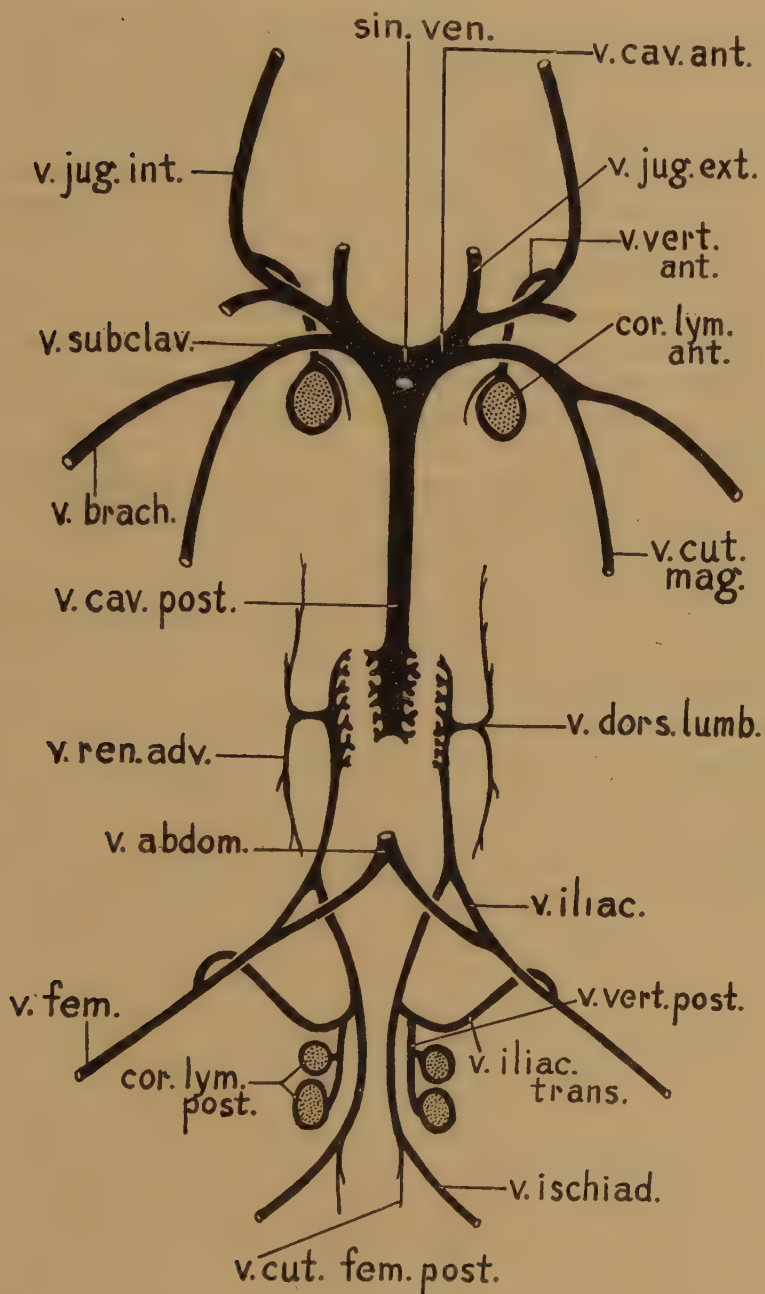


Figure 9

the lateral vein at the level of its 11th intersegmental branch (fig. 5). The proximal portion or junction of the latter branch with the postcardinal (*vena renalis advehens*) becomes the mouth or terminal segment of the posterior vertebral vein (*v. vert. post.*) and the caudal part of the lateral vein becomes its distal extension (figs. 7 and 8). A break occurring in the lateral vein between the two parts of it, referred to the longitudinal portion of the dorsolumbar and the posterior vertebral veins, respectively, establishes the independence of these two veins.

In the meantime the posterior lymph hearts have formed a connection with the corresponding posterior vertebral veins, so that these channels now become the outlet of the lymphatic drainage of the posterior region of the body. The shifting of the mouth of the posterior vertebral vein back along the ischiadic vein up to the point where the transverse iliac vein is forming is clearly indicated in figures 7 and 8. These diagrams show how easily the variations that are so common arise by the expansion, reduction, or persistence of different segments of the originally symmetrical intersegmental veins, resulting in different relations with the main venous trunks.

The degree of displacement, during development, of the various components of the venous conduit system, brought about by the more rapid elongation of some and the suppression of others, may be readily determined by comparing the successive stages with reference to the relatively fixed positions of the spinal ganglia, as indicated in the diagrams.

Resumen por el autor, H. E. Jordan,
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Estudios sobre la estructura del músculo estriado.

VII. El desarrollo del sarcostilo del músculo alar de la avispa,
con consideraciones sobre la base fisicoquímica
de la contracción.

La estructura del sarcómero del relativamente grosero sarcostilo del músculo alar de la avispa suministra la base de un intento de explicación fisicoquímica consistente sobre la contracción muscular. Las metafibrillas extremadamente pequeñas que constituyen este sarcostilo, homólogo de la miofibrilla del músculo estriado de los vertebrados, exhiben durante la contracción exactamente los mismos cambios estructurales que la fibra muscular estriada voluntaria en conjunto. El cambio esencial durante la contracción se refiere a la división igual de la substancia fuertemente tingible del disco Q al nivel del mesofragma y el movimiento de las mitades resultantes en direcciones opuestas, aplicándose contra los telofragmas terminales del sarcómero, donde se forman las bandas de contracción. La causa de la contracción muscular está localizada en este movimiento de cristaloides entre las partículas coloidales (submicras) de los segmenos claros terminales. El acortamiento y aumento de espesor de los sarcómeros durante la contracción se interpreta como el resultado de un cambio en la forma de las partículas coloidales intrafibrilares que pasan de la forma elipsoidal a la esférica, a causa de un aumento en su tensión superficial resultante de la disminución de sus cargas eléctricas superficiales, la cual sigue al paso de electrolitos entre ellas durante el movimiento de la substancia fuertemente tingible desde el mesofragma a los telofragmas.

STUDIES ON STRIPED MUSCLE STRUCTURE

VII. THE DEVELOPMENT OF THE SARCOSTYLE OF THE WING MUSCLE OF THE WASP, WITH A CONSIDERATION OF THE PHYSICO- CHEMICAL BASIS OF CONTRACTION

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THIRTEEN FIGURES (TWO PLATES)

INTRODUCTION

In the last number of this series of studies⁹ it was shown that the constituent sarcostyles of the wing muscle of the wasp exhibit the same changes during contraction, with respect to the cross-striations, as do the complete fibers of striped muscle generally, namely, a reversal of striations as regards a deeply staining substance of the dim disc. It was assumed that the relatively coarse, cylindric sarcostyle of the wasp's wing muscle is the homologue of the more delicate myofibrils of vertebrate striped muscle. If this assumption accords with the facts, then Schaefer's¹⁵ explanation of the appearance of a reversal of striations during contraction, as an optical illusion due to the accumulation of intersarcostylic fluid at the telophragma levels of relative constriction, must be erroneous. Moreover, the idea that this sarcostyle during functional contraction swells at the levels of the dim discs, thus producing a relative constriction at the level of the telophragma, is itself erroneous. As was shown in the previous number,⁹ the beaded condition of the sarcostyle is the result of an artificial contraction following the osmotic action of a hypotonic medium. The functionally contracted sarcostyle, while it shortens and thickens, maintains meanwhile, nevertheless, a straight, unbeaded contour. None the less it seems desirable to establish definitely the actual morphologic status of the wasp's wing-muscle sarcostyle by a study of its development.

This is the primary purpose of this investigation, namely, to trace the developmental history of the wasp's wing-muscle sarcostyle with a view to determining its value in terms of the elementary myofibril of vertebrate striped muscle. The evidence which will be given below seems conclusive that the sarcostyle of the wasp's wing muscle and the myofibril of vertebrate striped muscle are actually strictly homologous elements. This being so, it follows that in our efforts to discover the ultimate physicochemical basis of contraction we may more profitably, and quite legitimately and confidently, confine ourselves to the relatively much coarser sarcostyles of certain insects' wing muscle (e.g., Diptera, Hymenoptera, and Coleoptera). The second purpose of this investigation is finally to attempt a physicochemical interpretation of the structural changes suffered by the sarcostyle during contraction, and to formulate a consistent hypothesis in explanation of the cause of muscle contraction. The entire series of these studies on muscle structure had for one of its chief objects the accumulation of sufficiently numerous and precise data for the establishment of a correct physicochemical interpretation of muscular contraction.

MATERIAL AND METHODS

The material available for this study consists of two fairly complete series of specimens ranging from the newly hatched larva to the older pupae, one series fixed in 95 per cent alcohol, the other in a 10 per cent solution of neutral formol. For this material I am indebted to Mr. Massie Page. For the purposes of the present problem we may confine ourselves to four salient developmental stages: 1) the oldest larval stage (or youngest pupal stage), namely, one in which the thorax is outlined and wing pads are discernible, but no external leg rudiments; 2) an intermediate white pupa; 3) a later gray, or slightly pigmented, pupa, and, 4) the black, almost mature, pupa. The thorax was embedded in paraffin. Sections were cut at 4μ , and stained with iron-hematoxylin, followed in some cases by eosin counterstain.

DESCRIPTION

In the youngest, legless pupal stages very delicate wings are already present. Serial sections through the thorax show the imaginal discs still in continuity with the ectoderm ventrocaudally. Here, then, occur the initial myoblasts (fig. 1, *a* and *b*). Older stages in the muscle histogenesis occur anterodorsally (fig. 3 and 4). Between these terminal levels occur intermediate developmental stages (fig. 2, *c*).

The initial myoblasts are long, fusiform elements with a vesicular, centrally located nucleus. The nucleus originally contains a single, dense, chromatic nucleolus. The latter subsequently divides, the nucleus now containing a pair of nucleoli. This condition foreshadows the ensuing direct nuclear division. The myoblasts fuse terminally, their tapering ends overlapping (fig. 1, *b*), to form the definitive muscle fibers. Meanwhile the nuclei multiply greatly by amitotic division. No mitotic figures were seen in the myoblasts or later muscle fibers at any stage. The muscle fiber accordingly arises by fusion of originally discrete cells, not solely and primarily by growth of the myoblasts. The nuclei multiply by direct division chiefly in planes perpendicular to the long axis of the myoblasts, thus forming axial columns of nuclei (fig. 1, *b*); but to some extent also by division in the longitudinal plane, thus originating more peripheral nuclei. Appearances like those illustrated in figure 2, *c*, represent in part the latter sort of division, but in part also no doubt levels of sections where the tapering ends of fusing myoblasts overlapped.

Already in the earliest myoblasts, like those of figure 1, *a*, an occasional peripheral myofibril is faintly discernible. The nature of this material does not permit of any definite statement regarding the origin of the myofibrils. I am unable to determine whether the original fibrils arise as such or by the alinement and subsequent coalescence of precursory myochondria. Nor can I be quite certain whether later fibrils arise by longitudinal division of preexisting myofibrils, or independently. I incline to think that the later myofibrils arise chiefly independently; at

any rate, there is no clear evidence of a longitudinal splitting. The fibrils soon extend uninterruptedly through several original cell limits, and they remain for a relatively long time homogeneous. In figure 2 (*a* and *b*) are illustrated transverse sections of myoblasts corresponding with *a* and *b* of figure 1. Illustration *c* of figure 2 represents an older myoblast. Connective-tissue cells occur among the myoblasts. At least some of these divide by mitosis. Many of these cells become fat-cells. The cell *c.t.* of figure 2 is at an early stage of differentiation into a fat-cell.

The earlier muscle fibers, formed by the fusion of myoblasts, grow rapidly in diameter (fig. 3). Both nuclei and myofibrils meanwhile undergo enormous numerical increase. In a transverse section (fig. 3) the nuclei, now granular and more chromatic, appear to be scattered at random. Longitudinal sections of fibers at this stage (fig. 4), however, show that the nuclei are arranged in long columns, in single or double file. The connective tissue cells have also meanwhile increased greatly in number. The interfiber spaces have a diameter approximately equal to that of the muscle fibers. These spaces are closely packed with stout, fusiform, and irregular connective-tissue cells. The latter subsequently differentiate largely into huge fat-cells. The myofibrils are still homogeneous and quite delicate. In transverse section they have the appearance of fine granules (fig. 3).

Passing now from the stage of the oldest larva to that of the white pupa, with well-developed wings and legs, the wing-muscle fibers are seen to have enlarged enormously (fig. 5). The nuclei are numerous, but of smaller size in transverse section than in the preceding stage. Longitudinal sections of such fibers (fig. 6) reveal the fact that many of the nuclei are now greatly elongated elements. These continue to divide amitotically. The fiber is enveloped by a delicate sarcolemma. In certain cross-sections the peripheral myofibrils appear to be arranged in radial lines (fig. 5). This is the sole evidence that myofibrils may in part arise by longitudinal splitting of preexisting fibrils. The myofibrils are now relatively coarse (figs. 5 and 6), but still clearly unstripped, and between the fibrils appears a very finely granular sarcoplasm (fig. 6).

Thus far there is no indication of even a telophragma. In a slightly older pupal stage (gray pupa), however, this membrane has made its appearance (fig. 10). The myofibrils, or sarcostyles, are now relatively very coarse, as may be seen by comparing figure 7 with figure 5 of the previous stage, and with figure 8 from the adult muscle. The stages of muscle development in the gray pupa are of the utmost significance in this connection. We meet here with the initial steps in the origin of the cross-striations due to the presence of dim discs. Certain large masses of fibers are composed of sarcostyles in which only the telophragmata have appeared (fig. 9, *a*). In other masses the sarcostyles contain also delicate, but deeply staining, Q-discs (fig. 9, *b*). In such sarcostyles the telophragma has changed to an only relatively faintly staining membrane. Still other large masses of fibers consist of sarcostyles with relatively wide Q-discs (fig. 9, *c*). In certain other groups of fibers the Q-discs appear double (fig. 9, *d*), and occasional sarcostyles of such groups reveal very clearly constituent finer elements, the metafibrils (fig. 9, *e*). The clear indication of metafibrils, as in *e* of figure 9, may probably represent an artificial condition; but that the sarcostyles actually are composed of still finer fibrils seems demonstrated by the conditions which obtain where the muscle is attached to the hypoderm (fig. 10). Here the sarcostyles appear to break up into very fine 'tendinous' fibrils. The transition from muscle to tendon appears to be through direct continuity of muscular metafibrils and tendon fibrils. The latter stain deeply in very dilute solutions of eosin, in contrast with the muscle which remains unstained. The metafibrillar composition of the sarcostyles is a point of cardinal significance with respect to the physicochemical explanation of contraction, and will be fully discussed below.

The order of development of the cross-striations here disclosed is also a fact of much importance. The Q-disc appears only after the telophragma becomes discernible. The Q-discs are at first only very delicate, and only gradually attain their typical width between successive telophragmata. Coincident with the appearance of deeply staining Q-discs, the telophragmata suffer

a diminution of staining intensity. The meaning of the double condition of the Q-discs, as in figure 9, *d*, is uncertain. It may have the same significance as in the mature sarcostyles, namely, indicative of an early phase of contraction.

The foregoing observations are specially significant by reason of the light they throw on the question of the function of the telophragmata. The data strongly suggest that the telophragmata furnish the pathways along which are transported the materials which contribute to the formation of the dim discs, as well as the materials which supply the nutritive demands of the sarcostyles. The genetic order of events here revealed explains the horizontal alinement of striations in cross-striped muscle. This matter also will be reverted to and more fully discussed below.

Thus far no evidence appears, either in the formalin or alcohol-fixed preparations of sarcosomes. The latter appear first in formalin-fixed muscle of the almost mature black pupa (figs. 11 and 12). A largely lipoid nature of these sarcosomes is suggested by the fact that they entirely disappear in muscle of this stage fixed in 95 per cent alcohol. The sarcostyles have attained almost their definitive diameter (compare figs. 12 and 8 and figs. 11 and 13). In longitudinal sections (fig. 11) the sarcosomes appear spheroidal, but transverse section at this stage reveal the fact that they are already laterally somewhat compressed, and so possess short, blunt, lateral wings (fig. 12). Generally only two sarcosomes occur to an intertelophragma space, indicating that the telophragmata offer an effective barrier against their passage through these levels, and suggesting that the materials for their elaboration were also transported through the telophragmata, a sarcosome each being contributed by one telophragma. Comparison of figure 12 with figure 8, the latter from an adult muscle, shows that the sarcosomes undergo considerable subsequent growth, a circumstance involving still greater compression between adjacent sarcostyles, with the formation of longer, thinner wing processes. The relatively late origin of the sarcosomes, that is, just prior to functional activity of the wings, suggests a close relation between

sarcosomes and the metabolic requirements of the relatively very rapidly contracting wing muscle.

In figure 13 are illustrated three successive stages in the contraction of the sarcostyle of the wing muscle fiber of an adult wasp. The sarcostyle *a* is in a condition of repose. The sarcostyle *b* is at an early phase of contraction. The Q-disc has become bisected by the appearance of an H-disc. The deeply staining substance of Q is accumulating at the levels nearest the telophragmata. The sarcostyle *c* is at a still later phase, when the deeply staining substance of the sarcoplasm has aggregated about the telophragma, so that now this membrane bisects a dark disc, instead of bisecting a light disc as previously. A true reversal of striations, as regards this deeply staining constituent of the sarcoplasm, has been effected. Sarcostyle *d* is in almost complete contraction. The sarcostyle has become thicker, and the sarcomeres relatively shortened. The deeply staining substance about Z in sarcostyle *c* has here condensed so as to form a contraction band of the contracted fiber. The double nature of this band is clearly shown in sarcostyle *d*. The telophragmata are, however, no longer discernible. The optical disappearance of the membrane Z in sarcostyle *d* is interpreted as resulting from the thickening of the sarcostyle, effecting thus a drawing out radially and a consequent thinning of this membrane to a point where it is no longer within the range of microscopic vision.

The above seriation of stages in contraction of the adult sarcostyle gives the key for the interpretation of figures 11 and 9, *d*, of immature sarcostyles. Sarcostyle *d* of figure 9 would thus appear to be in an early stage of contraction, the sarcostyle of figure 11 at a later stage corresponding with that of *c* of figure 13. Apparently the immature sarcostyles are capable of some degree of functional contraction even before the wings are moved in flight.

DISCUSSION

The foregoing description shows that the wing-muscle fiber of the wasp is essentially homologous with voluntary striped-muscle fibers generally. The fiber is a multinucleated structure resulting from the fusion of originally discrete myoblasts, and subsequent growth, accompanied by an increase in the number of myofibrils and by the amitotic multiplication of the nuclei. The fibrils first appear as homogeneous elements, which only later become cross-striped. The wing muscle of the wasp, as that of Hymenoptera, Diptera, and Coleoptera generally, differs, however, from the usual type of voluntary striped muscle, in the definitive stages of its differentiation, in that its fibrils grow to relatively enormous radial dimensions. But the developmental history of this relatively very coarse sarcostyle demonstrates its strict homology with the more delicate myofibrils of vertebrate skeletal muscle.

The question then arises concerning the functional significance of the relatively coarse sarcostyle of certain insects' wing muscle. Clearly the coarse, cylindric condition of the sarcostyle bears no direct causal relation to flight as such even among insects, since in the Orthoptera and certain Odonata the wing muscle fibers of the thorax are characterized by lamellar 'sarcostyles' with constituent very delicate myofibrils. When we seek for a possible explanation of the difference in girth of sarcostyles in the several groups of insects, we note the fact that what distinguishes the flight of Diptera, Hymenoptera, and Coleoptera from that of the Orthoptera, for example, is not so much the rapidity of flight as the ability on the part of the former groups to sustain rapid flight for relatively long periods of time. The suggestion then presents itself that a relatively coarse type of sarcostyle, characteristic of wing muscle of which is demanded long-continued function, may somehow better subserve the conditions of this demand than a structure characterized by relatively delicate cylindric or by lamellar sarcostyles. Such hypothesis is supported also by the fact that the sarcostyles of the analogous pectoral muscles of the humming bird and the bat are

relatively coarse cylindric structures. However, all speculations along these lines lose plausibility in view of the definite fact that also the coarse, apparently unitary, sarcostyles of wasp wing muscle resolve themselves finally into extremely minute constituent fibrils (metafibrils). This is true also of the lamellar type of wing muscle sarcostyle (e.g., mantis⁸). It might then perhaps be argued that the coarse, so-called sarcostyle of the wasp's wing muscle is not actually the homologue of the myofibrils of, for example, human leg muscle, but in fact represents a fascicle of such fibril homologues. The apparent force of such argument, however, is neutralized by the fact that also the myofibrils of mammalian skeletal muscle may be seen to consist of collections of still finer fibrils. The sarcostyle of the wasp's wing muscle differs, moreover, from the lamellar, so-called sarcostyle of Orthoptera, in that the latter includes relatively fewer constituent fibrils and relatively much larger quantities of intra-sarcostylic non-fibrillar sarcoplasm. Successively more detailed analysis of muscular fibrils reveals successively finer constituent meta-fibrils up to the limits of visibility. As above described, however, and already explained, the early stages in the development of the wasp's wing-muscle sarcostyle show that it is strictly homologous with the myofibril of vertebrate striped muscle. Clearly, also, rapidity of function, or long-sustained function, is not directly related to complexity of cross-striation; for the wasp's wing muscle, and vertebrate cardiac muscle, is characterized by a relative simplicity of striation. Complexity of striation, resulting from the presence of an additional N-disc, as in insect leg muscle generally, would thus appear to be related to force of function rather than to rapidity or long continuance of function.

Insect wing muscle generally, however, differs from voluntary striped muscle of vertebrates in the occurrence of numerous, relatively large sarcoplasmic granules or sarcosomes in the former. But comparable elements occur also in the analogous pectoral muscles of bats and birds (Thulin¹⁶), and in mammalian heart muscle (Bullard¹). The common factor in the conditions underlying the peculiar function of these three types of muscle is the

ability of long-sustained function. The evidence suggests that large and abundant sarcosomes subserve the peculiar metabolic needs of muscles which act continuously for long periods of time. The absence generally of at least large and abundant sarcosomes in insect leg muscle, and in vertebrate skeletal muscle generally, suggests that forceful function only at intervals does not necessitate exactly the same type, or at least the same degree, of support of its metabolic requirements.

The sarcosomes develop relatively late. They appear first in the almost mature (black) pupa (fig. 11). They are at first spherical in shape; subsequently they become modified into winged elements, the result of mutual pressure between the adjacent growing sarcostyles and the enlarging sarcosomes. As was suggested in a previous article,⁹ the winged type of sarcosome probably largely persists throughout the life of the individual. Microchemical evidence was also given indicating that, besides a predominant lipoid constituent, the sarcosomes, at least in the later phases of elaboration, include an additional substance, possibly a carbohydrate. The very definite arrangement of the first formed, spherical sarcosomes, two to each sarcomeric interval, suggests that the material for their elaboration enters the intersarcostylic spaces via the telophragmata.

A detail in muscle histogenesis about which there has been much confusion and unprofitable speculation concerns the fact of the regular horizontal alinement of identically differentiated levels of the cross-striped myofibrils of a striped muscle fiber. The question arises as to how these alternating discs of adjacent fibrils are first brought into horizontal alinement. If the cross-striped myofibrils arise originally independently of telophragmata, as the illustrations of Godlewski^{2,3} and of Luna¹¹ for example, purport to indicate, then it is almost inconceivable how they may subsequently be brought into horizontal alinement. Whatever idea different investigators may hold regarding the origin of the initial myofibrils in various instances, whether as fibrils, mitochondria, or as prefibrillar myochondria which subsequently coalesce to form fibrils, all agree that the first genuine myofibrils are originally apparently homogeneous and only sub-

sequently become cross-striped.¹ The illustrations of Godlewski, while showing cross-striped myofibrils unconnected by telophragmata in young myoblasts of mammals, give no indication of how the secondary myofibrils originate. Possibly Godlewski failed, or was unable by reason of their extreme tenuity, to see the telophragmata actually spanning the interfibrillar spaces among the original myofibrils. Be this as it may, we possess two definite observations which explain how this transverse alinement of identically differentiated levels of the myofibrils of a muscle fiber is produced.

The clearest evidence concerning this point accrues from the present investigation. It seems perfectly plain in this material that telophragmata precede the appearance of Q-discs (figs. 9 and 10). It was shown in previous papers^{5,6} that the telophragmata are intimately connected with the sarcostyles and with the peripheral sarcolemma. In this way each sarcostyle is brought into relation with the interfiber tissue spaces and thus with the nutritive tissue fluid. Assuming that the telophragmata are pathways for the entrance and exit of materials between the

¹ M. R. Lewis, however, claims that in the myocardium of the chick embryo it can be demonstrated by a certain fixing and staining technic that the 'fibrils' are completely cross-striated from their first appearance (Johns Hopkins Hospital Bulletin, vol. 30, p. 1). Moreover, she interprets the 'fibrils' as fixation products, a view long since urged for striped muscle generally by Van Gehuchten (La Cellule, T. 4, p. 247, 1888), but never widely accepted. The cross-striations she regards as genuine fundamental structural features of the myoblast as a whole. If the conclusion here reached with regard to the artificial nature of the fibrils of the primitive myocardium of the chick were applied to the wing muscles of the wasp, we would be obliged to interpret the sarcostyle (homologue of the vertebrate myofibril, as above demonstrated) of the latter muscle as a developed and differentiated fixation product; since, no one I suppose, would seriously attempt to explain this definitive sarcostyle of adult wing muscle of wasp as also an artifact. It may be suggested that the reason why the primitive myofibrils described by certain investigators in cardiac muscle are not discernible microscopically in living myoblasts is not because they are not actually present, but because they are relatively fluid and because in consequence the refractive index of their sarcoplasm is so close to that of the interfibrillar sarcoplasm that the contrast between the two is insufficient to permit of clear differentiation under the microscope. The coagulative effect of fixation may bring about a greater relative difference between the refractive indices of the two sarcoplasmic colloids, and so render visible the denser fundamental sarcoplasmic fibrils.

sarcostyles and the interfiber tissue spaces (and this would appear to be their chief function), it becomes clear why the secondary modification of the originally homogeneous sarcostyles, namely, the formation of the Q-discs, follows the development of the telophragmata. Such genetic course explains at once the reason for the maintenance of a strict transverse alinement. The investigations of Macallum¹² and of Menten¹³ have shown that the dim discs contain potassium salts, chlorides, and phosphates. The presence of these substances in these regions may be the reason for their deeper staining capacity. These substances, considered physicochemically, are soluble crystalloids, at least in part electrolytes, and their segregation in the middle of the colloidal sarcomeres against the mesophragma, after entrance is thus explained.

The difference in staining reaction of the telophragmata at the several successive early stages in the development, from the viewpoint of the relative amount of Q-substance, supports the idea here advocated, namely, that the materials for the production and growth of the Q-discs enter via the telophragmata. In figure 9, *a*, the telophragmata are relatively coarse and stain deeply. In *b*, where a thin Q-disc has appeared, the telophragmata are now delicate and relatively pale. The sarcostyle *a* may be interpreted as at the stage where the telophragmata are saturated with the deeply staining material, which in *b* has become segregated in the delicate Q-disc. To the latter is later added more of similar material to produce the relatively thick Q-disc of sarcostyle *c*. In view of the fact that the sarcostyles are closely connected with the telophragmata, the subsequently stratified sarcostyles (differentiating in the manner indicated through segregation of crystalloids entering the colloidal sarcomeres through the telophragmata) must of necessity hold their alternating strata in horizontal alinement.

The other pertinent observation in this connection concerns the mode of the development of the myofibrils in the body muscle of the newly hatched rainbow trout.⁸ The same histogenetic series of events in trout has been described also by Heidenhain.⁴ Here the myoblasts originally contain a single, coarse, homo-

geneous, deeply staining, cylindric myofibril lying close to the nuclear wall within the cytoplasm. The origin of this initial sarcostyle could not be determined. This primordial sarcostyle produces four secondary sarcostyles by two practically simultaneous longitudinal divisions. These secondary sarcostyles assume a stout lamellar form, and subsequent sarcostyles arise only by successive radial and central longitudinal fissions. Thus while the sarcostyles, both peripheral lamellar and central cylindric, become cross-striped during the early stages of histogenesis, all subsequent myofibrils must maintain a similar alinement of their different alternating strata by reason of their origin by longitudinal division of already striped fibrils and their continued interconnection through the original telophragmata. Telophragmata are discernible following the first division of the initial sarcostyle. The available definite evidence therefore indicates that the cross-striations, as regards the Q-discs, only follows the appearance of telophragmata connecting with the peripheral sarcolemma, and so with the interfiber tissue spaces; and that the stratification results from the intake via the telophragmata of soluble crystalloids which become segregated in the Q-disc.

The foregoing descriptions and discussions, together with the data comprised in the previous papers of this series, lead naturally to an attempt to formulate a correct interpretation of the structural changes which the sarcostyle undergoes during contraction, in terms of physicochemical factors, and to an effort to explain muscle contraction in terms of these changes. The specific central problem narrows itself down to a question of the intimate structure and physical chemistry of the contracting single sarcomere of the relatively coarse sarcostyle of the wasp's wing muscle.

The sarcomere is bounded at both ends by a true membrane, the telophragma. Its middle is occupied by a disc of variable width, the so-called Q- or dim disc. This disc is composed of a substance which appears darker in unstained preparations, and which takes a deeper stain in fixed preparations treated with basic dyes. It contrasts in these respects with the lighter por-

tions, halves of so-called J- or clear discs, intervening between it and the terminal telophragmata. The sarcomere is bounded peripherally by a layer which has the properties of a semipermeable membrane, as demonstrated by its response to hypo- and hypertonic salt solutions. This layer, the sarcostrylic membrane, is intimately connected with the telophragmata. Bisecting the Q-disc there occurs a delicate dividing structure, presumably a membrane, as demonstrated by the equal division of this disc in contraction along the midline, the mesophragma. This membrane, however, is not discernible as such in this sarcomere under the highest powers of the microscope. Minute analysis reveals the fact that the apparently homogeneous sarcomere consists in fact of ultimate metafibrils. The latter are intimately attached to the telophragmata. Macallum¹² and Menten¹³ have shown that the Q-disc contains segregated chlorides, phosphates, and potassium salts. The presence of these substances in this area presumably accounts for the 'dim' appearance and the deeper staining capacity, possibly also for the relatively greater anisotropy, of this disc in contrast with the terminal J-segments. These salts represent soluble crystalloids, therefore, at least in part, electrolytes, and give to the Q-disc a composition physico-chemically different from the predominantly colloidal terminal clear portions. The sarcomere, therefore, consists of a cylinder of minute fibrils enveloped by a peripheral membrane, each colloidal fibril containing medially a mass of segregated crystalloids. Through the terminal telophragmata of the sarcomere, each fibril (metafibril) is placed in capillary relation with the intersarcostrylic fluid spaces. Presumably there exist between the metafibrils capillary interfibrillar canaliculi. When the muscle contracts, the predominantly crystalloidal medial disc (Q-disc) of each metafibril of the sarcostyle divides along the midline (mesophragma level) and the resulting halves move in opposite directions to fuse with similar halves, from successive sarcomeres, along the terminal telophragmata, thus forming contraction bands. The contraction bands accordingly represent discs of predominantly crystalloidal composition, and a reversal of strata (striations) as regards the deeply staining crystalloidal substance of the relaxed sarcostyle has occurred during contraction.

The problem of muscle contraction, therefore, resolves itself, in the final analysis, into a physicochemical explanation of the shortening and thickening of the sarcomere in relation to the movement of a medial mass of crystalloids (electrolytes) through the terminal colloidal segments against the telophragma boundaries. It is here assumed that the movement of crystalloids among colloids is the cause, not simply the accompaniment, or the result, of contraction.

The solution of the above-stated problem involves also an explanation of why, during the original determination of the stratified condition of the sarcolemma, the crystalloids, presumably entering terminally via the telophragmata, take a definite median position. The attempt at such explanation must first be disposed of. In regard to this aspect of the complete problem, we are actually dealing with a colloidal compartment, a hydrogel of myosin, bounded on the side where the crystalloidal substance presumably enters by a relatively coarse telophragma, at the opposite end where it is deposited, by a relatively delicate mesophragma. When crystalloids mingle with a colloid, the molecules of the latter suffer a change of surface electrical charges, and it may be assumed that the crystalloidal particles or ions are repelled (or perhaps simply passively carried by fluids, due to the fusion of colloidal particles behind thus propelling fluids forward) to the limit where they are held by the mesophragma and the adjacent mass of electrolytes.² The electrical condition of the now polarized sarcomere may now be considered to be in stable equilibrium in the resting fiber. Whatever the original form or state of aggregation of the colloidal particles, the passage of the crystalloidal particles, and their

²The manner of origin of the initial stratification may perhaps be comparable to that of the so-called Liesegang phenomenon of colloidal chemistry, which phenomenon occurs when a gel containing a substance in solution is treated with a second solution capable of reacting with the solution in the gel; e.g., when to a test-tube partly filled with 1 per cent agar gel containing calcium chloride is added a solution of sodium carbonate. The calcium carbonate formed by the interaction is deposited in strata throughout the agar cylinder (vide Hatschek, "An introduction to the physics and chemistry of colloids," p. 73, P. Blakiston's Son & Co., 1919).

segregation in the future Q-disc, must be considered to cause the assumption of an ellipsoidal form of the colloidal particles with the long axis parallel to the length of the sarcostyle. Such original elongation of the colloidal particles may cause a certain amount of elongation or longitudinal growth of the prefunctional sarcostyle. A possible original change of form, under the influence of the entering crystalloids, from an ellipsoidal form (with long axis of colloidal particle parallel to length of fiber) to a spherical shape, would offer the same basis for a future contraction of the sarcomere, if we assume that the formation of the contraction band involves a change of form of the colloidal particles (due to alteration of surface tension) from a spheroidal form to an ellipsoidal form in which the long axis of the colloidal particle is placed at right angles to the long axis of the sarcostyle. All things considered, however, the former alternative seems the more probable.

We may now proceed to consider contraction in the histologically mature sarcostyle. Contraction is initiated by a nervous stimulus. The latter may be regarded as a wave of negative electricity. We may suppose that the negative charge enters the sarcomere at the level of the more delicate mesophragma. This disturbs the electrical potential and causes repulsion of the electrolytes; that is, the charged ions are made to travel from the level of the mesophragma through the adjacent colloidal area against the telophragmata, where contraction bands are formed. The movement of the electrolytes among the colloidal particles causes a change of surface energy, hence of surface tension, by reason of the discharge of surface electrical charges and in consequence a change of shape of the colloidal particles. If we assume that this change of shape is one of change from an ellipsoidal form (oriented in the longitudinal plane) to a spheroidal shape, the shortening and thickening of the constituent sarcomeres of the sarcostyles, and thus muscle contraction, is accounted for. The formation of the contraction band again results in a condition of stable electrical equilibrium, which latter is again upset when the particular nervous stimulus is interrupted, and a movement of the electrolytes is started in the opposite direction, resulting thus in the characteristic strati-

fication and the electrically stable condition of the sarcostyle in repose. If this is in fact the central significance of the deeply staining Q-substance, its variable relative width in different fibers of the same muscle becomes intelligible: its relative quantity within certain limits may not be a fundamentally essential requirement for adequate function of the contractile mechanism; all that may be required is a certain minimal amount and limitation within certain maximal amounts. Furthermore, the apparent relative amount of the Q-substance may be largely incidental to the degree of its concentration.

Since I have previously deduced and supported the hypothesis that intercalated discs, characteristic of heart muscle, and occasionally found also under certain conditions in voluntary striped muscle,⁷ represent in essence modified irreversible contraction bands, it seems demanded in this connection that the formation of these intercalated discs be also explained consistently with the above outline of muscle contraction. During muscle contraction lactic acid is formed. When a muscle is made to function to exhaustion, the amount of lactic acid is excessively increased. Acid has a precipitation or coagulative effect upon colloids and upon mixtures of colloids and crystalloids. Intercalated discs would thus find their explanation, in accordance with the above scheme of contraction, in the supposition of the production of a relatively excessive amount of lactic acid under certain conditions, sufficient to effect a precipitation, that is, an irreversible coagulation, of a part of, or an entire contraction band.

The above-outlined physicochemical explanation of muscle contraction is in essence very similar to that presented by Prenant, Bouin, and Maillard.¹⁴ These histologists describe contraction as an electrocapillary phenomenon. The cause of the shortening and thickening of the sarcomeres they also locate in a change of shape of the ultimate colloidal particles of the intra-fibril sarcoplasm, following an alteration of electrical potential of opposite surfaces of contact of adjacent particles. But these authors do not carry their analysis and interpretation to the point above indicated with regard to the first appearance and the segregation of the crystalloids within the primitive colloidal

sarcomere, nor do they recognize a movement of crystalloids during contraction from the mesophragma to the telophragma, nor do they locate the cause of change of shape of colloidal particles specifically in the surface of contact between electrolytes and colloidal particles.

Similarly Lillie's¹⁰ explanation of muscle contraction has a close resemblance to our hypothesis. However, Lillie conceives of the intimate structure of the sarcomeres in our opinion erroneously, in that he regards the dim Q-disc as the result solely of a greater concentration, or of a different state of aggregation, of colloidal particles at this level. This alleged constitution presupposes relatively large interstitial fluid-containing spaces in the clear J-disc. Nor does Lillie recognize a movement of dim substance during contraction. He does, however, assume a movement of interstitial fluid from *M* to *Z*, but only as an incidental result of the closer aggregation of the colloidal 'sub-microns' of the dim disc. Lillie conceives of the energy of contraction as transformed surface energy of the ultimate structural element or colloidal particle (submicron) composing the fibril gel. The shortening and thickening of the sarcomere is thought to result from the massing of the colloidal particles in the 'anisotropic' segments, the massing itself resulting from the heightened surface tension resulting from diminished electrical surface polarization. He regards contraction as similar to reversible coagulation of colloids. This hypothesis, considered in detail, gives no clue for the consistent interpretation of intercalated discs. It is readily conceivable that the conditions here postulated might lead to an irreversible coagulation of sarcoplasmic colloids; but such areas of irreversibly coagulated sarcoplasm would be at the level of the mesophragma, according to Lillie's explanation, and not, as is actually the case, at the levels of the telophragmata.

According to our hypothesis, on the contrary, the shortening and thickening of the sarcomere, that is, contraction, results from the change of shape of the ultimate colloidal sarcoplasmic particles following an increased surface tension, the latter resulting from decrease or disappearance of the surface charges of the

colloidal particles accompanying the movement of electrolytes among them from the mesophragma to the telophragma, the movement being initiated by the disturbance of electrical potential of the membranes, primarily of the mesophragma, surrounding the sarcomere following the passage of nerve stimulus. It must be admitted, however, that a precipitation of colloidal particles by electrolytes would have essentially the same effect of shortening and thickening of the sarcomere as would a change of shape of the particles. But Lillie's hypothesis permits of no plausible explanation of the dim character of the contraction band. If, as Lillie assumes, the Q-disc of the fibril in repose is 'dim' because of a closer aggregation of colloidal particles at this level, and if, as he further assumes, contraction is essentially a matter of a still closer massing of colloidal particles at this level, with a forcing of interstitial fluid into the telophragma borders of the clearer J-segments of the sarcomeres, then the latter areas should become lighter instead of becoming darker, as they actually do become as parts of contraction bands. If the Q-discs are 'dim' because of a closer aggregation of colloidal particles here, then the 'dimness' of the contraction bands should consistently be explained in the same way; but that the latter are areas of closer aggregation of colloidal particles is in contradiction to the central idea in Lillie's hypothesis. Reconciliation of this damaging contradiction can be effected, and the integrity of Lillie's hypothesis maintained, only on the assumption that the Q-disc is dim because of the presence here of an additional darker, more fluid substance, which latter becomes forced against the telophragmata during contraction and here gives the darker color or 'dim' appearance also to the resulting contraction band. But when this further assumption has been added to the basic assumptions of Lillie's hypothesis, we are very close to the hypothesis here urged and supported, namely, that the cause of contraction is located in the final analysis in the fact of a movement of 'dim' substance among the colloidal particles of the sarcomere from *M* to *Z*. And in view of the demonstration of the segregation of crystalloids in the dim discs (Q-disc and the contraction band) the latter hypothesis would seem to be the most satisfactory alternative.

No hypothesis of muscle contraction can of course be satisfactory that cannot be harmonized with the principle of the conservation of energy. We must be able to find within the muscle, sources of energy approximately equal in sum to the amount of energy expended by the functioning muscle; which energies must both be approximately equal to the underlying chemical energy of the metabolic processes of active muscle. The details of the exact relation between the chemical energy of muscle metabolism and the postulated surface-tension energy of the sarcoplasmic particles need not be here considered. The energy of the nerve stimulus need of course be only sufficient to start the initial link in the chain of chemical reactions of the metabolic processes underlying the assumed surface-tension energy of contraction. Lillie¹⁰ supports the hypothesis that the contractile energy of muscle is due to changes in surface tension of certain muscle elements by these statements:

In contraction the surface tension of these elements is supposedly increased. If this increase of tension is sufficiently great, and the area of the active surface sufficiently large, the transformable surface-energy, which is measured by the product of these two factors, may be sufficient to account for the work done by the muscle in contraction. There is good reason to regard the ultimate colloidal particles of the fibrils as corresponding to such elements. By their union to form larger particles, as in the general process of colloid-coagulation, sufficient mechanical energy to account for contraction might conceivably be freed, since the reduction of surface-area in such a process may be very great, implying a correspondingly large transformation of surface-energy (p. 252).³

In résumé, the gist of our hypothesis involves the following assumptions, which are consistent with the fact of a movement of 'dim' substance from the Q-disc to the contraction band during contraction: The nerve stimulus causes a movement of ions from *M* to *Z* effecting a change in shape of the colloidal particles from ellipsoidal to spherical; cessation of stimulus, an instant return of ions from *Z* to *M* with a return to the original ellipsoidal form of the colloidal particle; the change in form of the

³ For a review of the earlier literature touching similar interpretations of muscle contraction, the reader is referred to Lillie's paper and to Schaefer's textbook (p. 189).

latter being the result of an alteration of surface tension following alternating increase and decrease of surface electrical charges under the influence of the reversal of the direction of the current of action and the moving electrolytes.

The histologic data relative to the intimate structural changes in contracting muscle above given seem in strict accord with the conclusion that the source of the contracting energy of muscle resides in alterations of surface tension in the colloidal particles of the ultimate muscle fibrils. My conception of the physico-chemical process in ultimate detail differs from that of Lillie in essence only in that Lillie interprets contraction as the result of an aggregation or union (resembling reversible coagulation or precipitation) of the colloidal particles mainly in the Q-disc, with expression of interstitial fluid into the J-disc, following increase of surface tension due to decrease of surface electrical charges; while I view the histologic data (supplemented by the micro-chemical data of Macallum and of Menten) as indicating an actual movement of soluble crystalloids (electrolytes) from the mesophragma to the telophragmata, which movement of electrolytes may be interpreted as the chief factor in effecting an increase of surface tension of the colloidal particles and so altering the shape of the particles, which alteration of shape, rather than a massing of the particles, effects a shortening and thickening of the sarcomeres.

SUMMARY

1. The relatively very coarse sarcostyle of the wing muscle of the wasp is strictly homologous with the myofibril of vertebrate striped muscle. Both varieties of fibrils consist of bundles of extremely minute constituent metafibrils. The wasp's sarcostyle has an enveloping layer with the properties of an osmotic membrane, the sarcostylic membrane.

2. The structural changes exhibited by a striped muscle fiber during contraction are the result of similar changes in the constituent metafibrils. The fundamental and essential change con-

cerns the equal division at the level of the mesophragma, and the subsequent movement, of the more deeply staining substance of the Q-disc, against the terminal telophragmata of the sarcomere, where are formed the contraction bands.

3. The salient histogenetic steps occur in the following order: The myoblasts of the imaginal disc differentiate from ectoderm; the first-formed myofibrils are homogeneous; the telophragmata precede the appearance of the Q-discs; the latter are at first very delicate and only gradually acquire their typical definitive width. The sarcosomes appear only relatively late, shortly before functional activity of the wings.

4. The order of development of the two chief cross-stripes, the connecting Z-membranes and the Q-discs, explains the exact horizontal alinement of similarly modified levels of the constituent fibrils of a striped muscle fiber. The telophragmata probably function chiefly as the pathways along which the deeply staining substance of the Q-discs first enter the sarcostyle, and along which metabolic products pass to and fro between the sarcostyles and the interfiber tissue spaces.

5. In the effort to disclose the ultimate physicochemical bases of muscle contraction, we may legitimately and confidently confine ourselves to the structure of the sarcomere of the relatively coarse myofibril (sarcostyle) of the wasp's wing muscle. The fundamental factor in muscle contraction is located in the movement of the deeply staining substance of the Q-disc against the telophragmata in the formation of contraction bands. The concomitant shortening and thickening of the sarcomeres is interpreted as the result of a change in shape, from ellipsoidal to spherical form of the ultimate colloidal particles of the intra-fibril sarcoplasm, following an increase of surface tension of these particles (submicrons) resulting from a decrease of surface electrical charges due to the passage of electrolytes (crystalloids of the deeply staining substance of Q) among the colloidal particles.

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EXPLANATION OF FIGURES

The drawings were made from sections of tissue fixed in 10 per cent formalin. The sections were cut at 4μ , and stained with iron-hematoxylin. With the exception of figure 13, the magnification of the drawings is 1300 diameters. The section from which figure 10 was made was lightly counterstained with eosin.

PLATE 1

EXPLANATION OF FIGURES

1 *a*. Longitudinal section of myoblast immediately after separation from the imaginal disc. The originally single nucleolus has become divided in anticipation of the ensuing direct division of the nucleus. *b*, Three slightly older, now multinucleated myoblasts, in process of fusion to form a muscle fiber. Delicate peripheral myofibrils are faintly discernible. The specimen from which these drawings were made was at the latest larval or earliest pupal stage; wing pads were present, but the legs had not yet appeared.

2 *a*, *b* and *c*. Transverse sections of three successively older myoblasts from the same specimen as figure 1. Sections *a* and *b* correspond to *a* and *b* of figure 1; *c* represents a slightly older stage, cut at the level of lateral fusion as indicated by the two radially adjacent nuclei. *c.t.*, an interfiber connective-tissue cell in early stage of metamorphosis into a fat-cell.

3 Transverse section of later wing-muscle fiber from same specimen. The nuclei are now very numerous and scattered apparently at random. The myofibrils are uniformly distributed throughout the sarcoplasm and appear as darker dots in transverse sections. *c.t.*, a connective-tissue cell. The latter are very numerous and completely fill the wide interfiber spaces.

4 Longitudinal section of fiber like the one of figure 3. The homogeneous myofibrils are conspicuous between the columns of nuclei. The interfiber spaces are approximately of the width of the diameter of the fibers. These spaces are completely filled with short fusiform and polyhedral connective-tissue cells.

5 Transverse section of older fiber, from white pupa (with wings and legs). The fibrils have become much coarser and appear radially disposed along the left border.

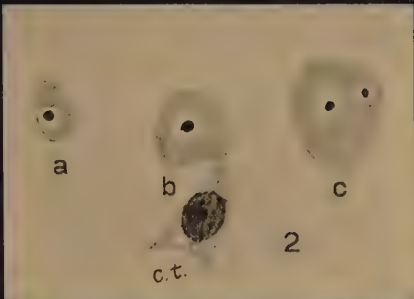
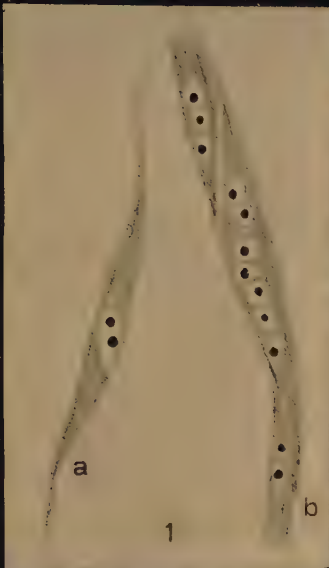


PLATE 2

EXPLANATION OF FIGURES

6 Longitudinal section of fiber like that of fig. 5. The nuclei are long narrow elements dividing directly into smaller nuclei. Among the homogeneous coarse myofibrils are scattered smaller irregular granules. There is as yet no indication of telophragmata or other stratification in the fibrils.

7 Peripheral portion of older fiber in transverse section, showing the coarse myofibrils (sarcostyles), a peripheral nucleus, and the sarcolemma. Sarcosomes have not yet made their appearance. The section is of a later pupal stage (gray pupa).

8 Portion of adult wing-muscle fiber in transverse section, showing the coarser myofibrils and six included irregular sarcosomes.

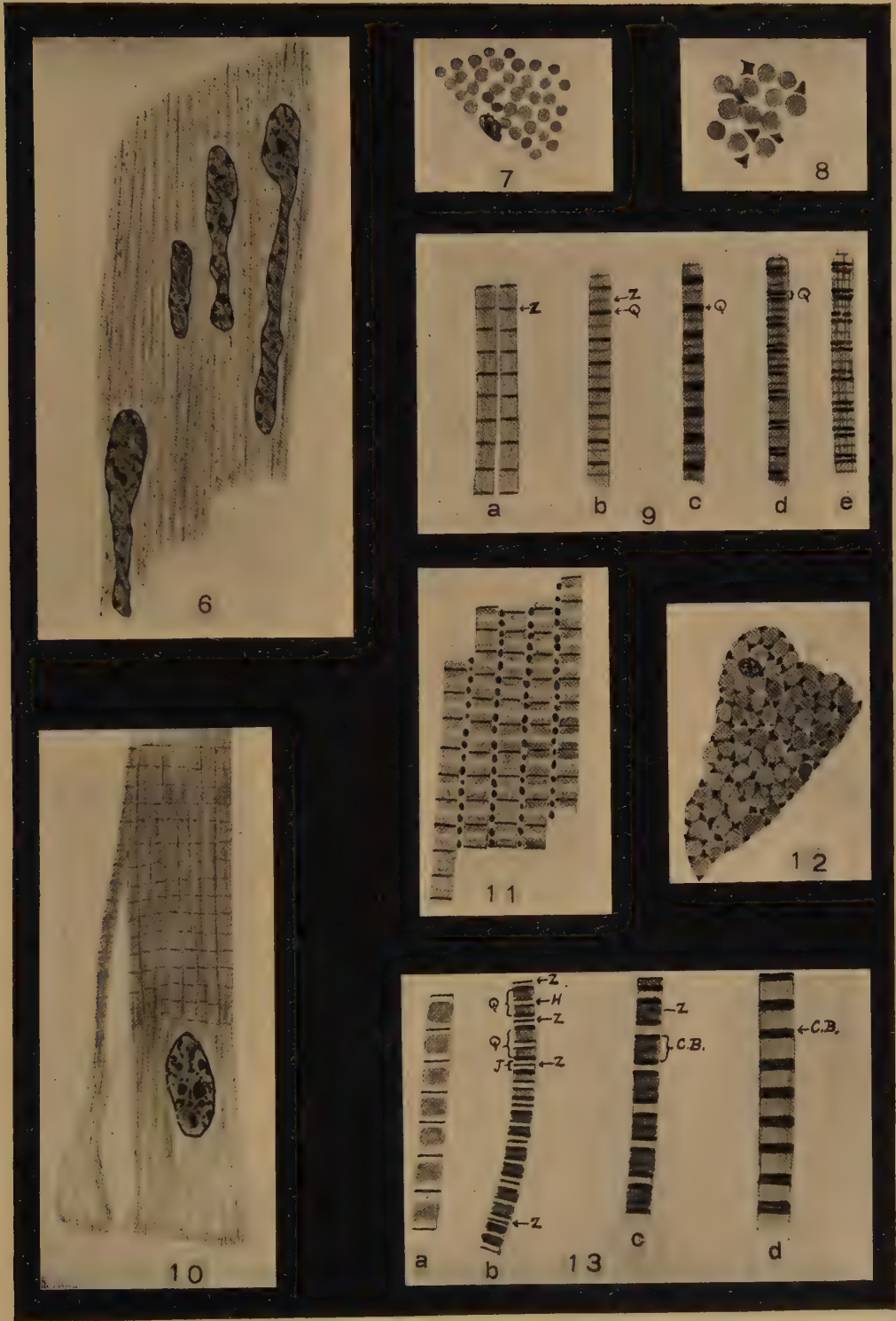
9 *a, b, c, d* and *e*. Three successive stages in the later development of the myofibril, from a longitudinal section of the thoracic (wing) muscles of a gray pupa (same as fig. 7). *a* shows two adjacent fibrils in which only the Z stripe (telophragma) has appeared. This stripe stains very intensely at this stage. In fibril *b* the Z-stripe is faint, and a deeply staining but thin Q-disc has appeared. In *c* the Q-disc has become much thicker. *d* and *e* are at the same stage of development, but in *d* the Q-disc has become bisected and an H-disc has in consequence appeared, and in *e* the metafibrillar constituent elements of the sarco-style have become conspicuous.

10 Longitudinal section through region of attachment of muscle to epidermis. The nucleus lies in the 'tendinous' portion of this connection. This tendinous portion stains much more deeply in a very dilute eosin counterstain than the muscle. At the levels where the sarcostyles break up into the 'tendon fibrils' the telophragmata disappear.

11 Small area of longitudinal section of wing-muscle sarcostyles of older (black) pupa. Between the sarcostyles are single rows of small oval sarcosomes, generally two to a sarcomeric interval.

12 Portion of a transverse section of a fiber like that of figure 11, including one nucleus. Many of the apparently oval sarcosomes are now seen to have lateral wing-like processes. Compare with figures 7 and 8.

13 Sarcostyles of definitive wing muscle of adult wasp at four successive stages in contraction. Fibril *a* is in repose; *b* is in an early, *c* in a later stage of contraction; *d* represents a contracted fibril with almost fully formed, double contraction band.



Resumen por la autora, Kaethe Weller Dewey,
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Contribución al estudio del sistema linfático del ojo.

La autora considera a la coloración vital como el mejor medio para demostrar los capilares linfáticos y espacios linfáticos del ojo, del mismo modo que los de otras partes del cuerpo. Las células endoteliales que tapizan estos canales tienen la propiedad de teñirse con el colorante vital. Los resultados de los experimentos con la parafenilendiamina hacen resaltar las diferencias entre los espacios de los tejidos y los espacios linfáticos, el plasma y la linfa propiamente dicha. Las observaciones llevadas a cabo mediante el teñido vital con referencia a su significación presunta en el sistema linfático no están en contradicción con los hechos anatómicos reconocidos. Aceptando el hecho de que las células endoteliales vitalmente teñidas denotan la presencia de canales linfáticos, se comprueba la ausencia de dichos canales en la córnea, mientras que la conjuntiva los posee abundantes. La esclerótica posee muy pocos capilares linfáticos, que a veces faltan en absoluto; pueden acompañar a los vasos sanguíneos que la atraviesan. Tampoco existen en la retina. La coroides los presenta principalmente en los coriocabilares. La glándula lagrimal, el tejido orbitario y los párpados presentan abundantes capilares linfáticos. No existen en el cartílago tarsal de los párpados. Las células vitalmente teñidas son mas abundantes en el cuerpo ciliar y, especialmente, en los procesos ciliares, que en cualquier otra parte del ojo. Esto coincide probablemente con mayores actividades funcionales, tales como la intensa participación en la secreción del fluido intraocular. El iris está provisto de escasos capilares linfáticos, a pesar de su rica irrigación sanguínea. Esto indica que tal órgano no desempeña las mismas actividades funcionales que el cuerpo ciliar.

Translation by José F. Nonidez
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A CONTRIBUTION TO THE STUDY OF THE LYMPHATIC SYSTEM OF THE EYE

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THREE FIGURES

In view of the great interest which evidences of an etiological relationship between infectious processes about the teeth and pathological conditions in other regions are receiving in recent years, clinical and anatomical investigations vie with one another in furnishing the necessary scientific foundation for more or less empirical conclusions. Relations between certain affections of the eye and diseased teeth have been recognized since the remotest ages, but reliable reports of actually observed transmissions of pathological processes from the teeth to the eye are all of a relatively late date. The number of these published reports is not inconsiderable.¹ Little, however, is yet known concerning the routes of transmission that could in any way be considered as positive and final. The dental origin of cases of the so-called dental eye fistula, orbital phlegmon, and abscesses is revealed chiefly through the fact that the eye conditions either promptly disappeared with treatment of the involved teeth or that they developed upon the extraction of a tooth with or without involvement of the maxillary sinus. The traveling of the pus from diseased teeth to the orbit, as, for example, in phlegmon, has often been represented as being per continuitatem along the outer surface of the maxilla over the orbital border. Frequently a transmission by way of the veins is assumed, and also a few casual suggestions occur in the literature that the processes may progress by way of the lymphatics. The latter route, however, is probably more important and much more frequent than the

¹ A report of clinical observations along these lines will be published in *Archives of Ophthalmology*, July, entitled "Affections of the Eye from Diseased Teeth."

scanty and incomplete statements concerning it would make us believe.

The demonstration of direct communications between the lymph supply of the dental region and that of the eye is obviously difficult. In previous experimental work for the demonstration of the lymphatics of the dental pulp and the peridental membrane^{1,2} indications of extensive anastomoses in the lymph-supply of these two regions were sometimes incidentally obtained. In injections by the Gerota method of Prussian blue into the gum tissue the fluid was not only forced through the bony tissue of the jaw into lymph-vessels of the peridental membrane, but sometimes deep and superficial lymph-vessels of the infraorbital region were also injected. The looseness of the orbital tissue makes injections in the region of the eye unsuitable for purposes along these lines: the injection mass will follow the direction of the least resistance and fill the loose tissue of the orbit. This occurs also in injecting the fluid through the infraorbital foramen, which is the most accessible place for reaching lymph-vessels in either direction to the eye as well as the dental region.

Until recently our knowledge of the lymph-supply of the eye region was very limited and it is still quite incomplete with regard to the lymphatic system of the eye proper. Bartels,³ in 1909, writes: "Nowhere besides in the lids and the conjunctivae have genuine lymph-vessels been surely demonstrated, while we may say that it has been shown with a probability bordering on certainty, that in the cornea, the lens, and the vitreous body they are completely lacking. In fact, we need not look for a current of fluid in a stable optic apparatus. It is quite different, however, in the other parts of the eye which constantly have to perform most important work and where therefore correspondingly active metabolic interchanges must be assumed a priori. They have not yet been demonstrated, however."

A lymphatic apparatus of the orbit has been demonstrated by Birch-Hirschfeld.⁴ That the existence of such a system may be presupposed has been claimed before him by some writers who are unwilling to consider the lymphangiomas of the orbit as heteroplastic formations; the occurrence of these speaks for the

presence of lymphoid tissue in the orbit even if in such minute amounts as to escape microscopical observation. By methods which, according to Birch-Hirschfeld, produce an increased lymph secretion or lymph stasis resulting in dilatation of the lymph-capillaries, this author believes he has seen distinct lymph spaces in the orbital tissue—in the lipoid tissue, the lacrimal gland, between the muscles, and in the neighborhood of the optic nerve and the periosteum. With his methods he could not demonstrate the direction in which the lymph flows off nor a connection with any lymph-gland. He believes, however, we may assume that communication exists between these spaces and the lymph-vessels of the nose, and that there is a connection between the orbital lymph system and that of the surrounding regions through the perivascular spaces about the vessels passing through the superior and inferior orbital fissures.

Histologically, the demonstration of the minute lymph-vessels of most organs is very difficult, if not altogether impossible. Post-mortem, they are practically virtual spaces and the endothelial cells lining them are in general indistinguishable from the slender nuclei of the surrounding connective-tissue cells. In order to distend them and thereby render them more amenable to microscopic study Birch-Hirschfeld employed a drug which is known in pharmacology and toxicology to produce chemosis and edema of the orbit, exophthalmus and increase of the intra-ocular pressure. This drug is paraphenylendiamine hydrochloride. He also made use of dionin, small pieces of which he introduced into the orbital tissue. The action of this drug is to cause dilatation of the capillaries and increase of the lymph excretion, and this is especially well demonstrated about the eye. Paraphenylendiamine, according to him, produces stasis of the lymph, and an increase of the secretion of the lacrimal gland, of the mucous secretion of the conjunctiva and the salivary glands. If a large dose is given, the edema of the orbit extends also to the face and the neck. Edema of the glottis is the final cause of death. Similar observations are reported by Grunert,⁵ Matsumoto,⁶ Puppe.⁷ The spaces in the orbital tissue and those in the lacrimal gland which Birch-Hirschfeld found dilated and filled

with fluid after diamine poisoning are believed by him to be lymph-spaces, and he states that in some of the larger and medium-sized spaces he found a distinct endothelial membrane.

These statements by Birch-Hirschfeld seemed to me of extreme importance. If the observations could be verified and his conclusions shown to be right, the use of paraphenyldiamine should enable me to prove the correctness of a view obtained from previous experimental work on vital staining, which, in the absence of more positive proofs, I could express only suggestively.⁸ Vital staining, I stated, may be the means of demonstrating the lymph-channels of origin in most organs of the body by exhibiting their endothelial cells which have an affinity for vital stains. Granting the correctness of Birch-Hirschfeld's observations, paraphenyldiamine should be a valuable aid in such investigations by demonstrating a lumen in such endothelial-clad lymph-channels.

I tested this drug on two dogs, two cats, ten rabbits, and ten frogs. The larger number of these animals were injected with lithium carmine previous to their treatment with the diamine poison. The results of these experiments will be reported in detail in another paper as a question dealing largely with pharmacology. They were disappointing to the extent that they contributed nothing to the main purpose of this study: the microscopical study of the tissues in diamine poisoning failed to reveal what I had expected to find. The dilated spaces in the edematous tissues are not lined with vitally stained endothelial cells. Most of them are simply surrounded by delicate fibers without any cellular elements; occasionally a slender nucleus may be seen in this wall, resembling as much the nucleus of a connective-tissue cell as that of a flat endothelial cell. Vitally stained cells may be seen near these spaces, but never so near as to justify the impression that they form any part of the wall. I am, however, not inclined to believe that these spaces are lymph-spaces, as Birch-Hirschfeld does, but consider them simply as tissue spaces and distended meshes in the connective tissue, nor do I regard the fluid as lymph proper, but as a serous effusion, plasma from the blood-vessels.

Sections from the edematous subcutaneous tissue of the face and over the lower jaw in rabbits show that all this tissue is split up into innumerable spaces and slits filled with fluid, to regard all of which as lymph-spaces, potential or actual, would not be reasonable. One of the chief effects of the drug seems to be on the blood-vessels, perhaps irritating the endothelial wall of the capillaries, and thereby rendering it more permeable. This is particularly noticeable in muscles of the eye. The bundles and fibers of the muscles are separated more than is normal; the fibers of the connective tissue in these intermuscular spaces are slit apart and all these widened meshes and spaces are filled with fluid, which stains well with hematoxylin. The muscles are richly supplied with blood-capillaries which wind in and out about the muscle fibers. But we fail to see any lymph-capillaries with a perceptible lumen; if they are present, as is to be presumed, they are at any rate not dilated. The muscles about the eye, like some muscles of the face, show a brown discoloration after diamine poisoning. It is an interesting observation that, while the anatomical and clinical effects of paraphenylendiamine are so widely different in the different species of animals, and even in animals of the same species, they all have one feature in common, viz., this brown discoloration of certain muscles of the face. Some of the writers who have studied the effect of this drug claim that the cause of the edema is to be sought for in the lacrimal gland. On the other hand, Puppe believes that the stasis edema is perhaps due to the formation of thrombi in the veins, and Kunkel⁹ also assigns to the blood-vessels and the blood a greater significance for the development of the intoxication edema. My observations agree with the latter view.

On account of the extensive anastomoses of lymph-vessels obstruction to the outflow of lymph does not readily occur. We may conceive of the action of paraphenylendiamine as follows: in subcutaneous injections the drug enters the lymph channels, thence it is carried into the blood, where it irritates the walls of the blood-vessels, possibly having an injurious effect on the endothelial cells of the capillaries. Transudation of the plasma occurs very rapidly, the fluid filling all the tissue spaces and sep-

arating the tissue elements. The function of the endothelial cells of the lymph-capillaries being not simply one of absorption of such free fluid, but probably one of a selective action, of an interaction of metabolic processes, the fluid is not taken up and carried off rapidly enough with the result that stasis-edema develops.

The formation of lymph is not, as was formerly believed, a mechanical process, i.e., one of simple filtration and diffusion, but is work essentially done by the organs themselves. The mechanical theory has been superseded by the cellular-physiological theory. The endothelial cells of the lymph-capillaries probably play a chief part in these processes. Although these capillaries end or begin as absolutely closed culs-de-sac, and the presence of a continuous endothelium represents a barrier between them and the surrounding connective tissue, "the relations between the vascular cavity and the connective-tissue spaces remain very close," as Delamere¹⁰ states, "and cellular immigration and osmotic exchanges may always take place and the capillaries fulfill their function of drains, and, if the observations of Renaut are confirmed, may even act as selective drains."

The value of paraphenylendiamine in conjunction with vital staining is, in my opinion, this, that it illustrates and supports the theory of a difference between spaces filled with tissue fluids and real lymph-spaces and lymph-capillaries, which constitute the channels of origin of the lymph system. Bartels,³ it is true, is rather skeptical as to any fruitful research along these lines. To him this much-debated question is largely a philosophical one; he writes: "The question concerning the origin of the lymph system and the development of the lymph stream from the flow of the tissue juices is a purely philosophical and not an anatomical one. This question and that of the endings of the blood-vessels should be eliminated from anatomical discussions." Nevertheless, the contemporary conception of the origin of the lymph system is emphatic in upholding the theory of an independence of the lymph-spaces and the tissue spaces, and of the absence of open communications between them, as also of a difference between plasma from the blood-capillaries and lymph proper.

This fact is also illustrated by the observation that injections into the submucous cellular tissue of the skin may fill the tissue clefts and tissue spaces and produce edema, but not fill the lymph-vessels. Similar observations may be made in injecting the blood-vessels with carmine gelatin; when the injection is continued under high pressure for some time, it may happen that the fluid portion of the injection mass is pressed through the stretched capillary wall and fills the tissue spaces producing edema without entering into lymph-vessels. In fact, I have never been able to fill lymph-vessels by way of the blood-vessels.

As a result of my observations from the experiments which I have made, I have come to the conclusion that the vitally stained cells within the connective tissue of organs represent the endothelial cells lining the capillaries of origin. By several writers the view has been expressed that the connective tissue evidently plays a much more important rôle than that of being simply a supporting stroma for other parenchymatous tissue, and this impression is imparted to them chiefly by the presence of these peculiar vitally staining cells which have been called rhagiocrines, resting wandering cells, macrophages, pyrrol cells, histiogenic wandering cells, etc. The ability of these cells to take up the vital stain apparently coincides with specific functional properties; they have chiefly been alleged with secretory functions, and Renaut¹¹ writes of the connective tissue as "the largest of the glands with an internal secretion which exists in the body of vertebras." On the other hand, Ehrlich points out the extraordinary adaptability of the cellular elements of this tissue and that a specific modification adjusted to definite functions of the organ which it supports, cannot be considered as in any way astonishing. But nowhere in the literature have I found even a suggestion that these specific cells may belong to the lymphatic apparatus. Yet we know that everywhere in the body the structures which constitute the beginning of the lymph system are embedded within the connective tissue. It is only reasonable to assume that the endothelial cells which form the sole wall of these delicate primary lymph-channels (lymph-spaces and lymph-capillaries) are more than a lining; that they are rather the chief

agents in taking up the ambient tissue fluid or plasma from the blood-capillaries after it has been altered in its contact with the cells. This process is more than one of simple filtration, or even of a selective filtration; it is a process of vital elaboration, including probably secretion and excretion. Furthermore, as the plasma differs from the lymph partially as a result of the activities of the blood-capillary endothelium, so, too, the lymph coming from these capillaries is again modified when passing through the lymph-gland; for there are distinct differences in the lymph entering the lymph-gland and that passing out of the gland. The latter shows an increase in the cellular elements; the tendency to fibrin formation and coagulation is more rapid, and the proportion of the water is diminished. This modification of the lymph is likewise the work of the endothelium of lymph-capillaries, for the lymph-vessels entering the lymph-gland break up into capillaries, thus forming a true portal lymph system. Bearing this in mind, it is most significant that this whole process of the formation of a second capillary network and of a modification of the lymph by its endothelium is signalized, as in the endothelium of the lymph-capillaries of the connective tissue, by the property of the cells to take up the vital stain. We have here, therefore, the striking phenomenon that at the source of the lymph system there are specifically functioning endothelial cells of capillaries, and that these alone have the power to take up the vital stain. This property is absent in the endothelial cells of the lymph-vessels arising from the capillaries, but is present again, and in a most marked degree, in the endothelial cells of the capillary network within the lymph-gland; these are most brilliantly stained, while the afferents and the efferents of lymph-glands have no vitally staining endothelial cells. Evans¹² also has pointed this out as a very striking phenomenon.

There are some other general observations on vital staining, agreeing well with anatomically established facts, to which I would call the attention. It is recognized that the lymphatics are unequally distributed throughout the organism, seemingly in an arbitrary fashion. The same observation is made in regard to vitally stained cells. Lymph-vessels are considered to be

absent in a few organs and tissues; these are the same organs in which these cells are lacking. They are however, present in certain regions where lymph-vessels have not yet been demonstrated because of the almost unsurmountable difficulty in injecting them, but where they may reasonably be assumed to exist.

The character of these cells has been interpreted variously; but the name of resting wandering cells seems to be the least fitting, for the most striking feature about them is the stability which characterizes their occurrence, their distribution, their arrangement, and their number. They are invariably absent or present in the same locality and invariably scanty or abundant in the same region. The constant recurrence of these features gives a strong impression that these cells are stationary and that they are part of some definite, functionating apparatus. As to the eye, the occurrence of the same unequal distribution in the various tissues is striking.

Schnaudigl¹³ has studied the effect of vital staining on the eye and made observations concerning the occurrence of vitally stained cells which are on the whole in accordance with my own. They are as follows: the lens is devoid of vitally staining cells. No such cells are found in the cornea, but the conjunctival tissue overlying the corneal tissue shows such cells in large numbers. Occasionally a long, slender, vitally stained cell is seen to extend from the conjunctiva into the cornea. The sclera contains such cells in scant number; it is not quite clear whether they belong to the tissue proper or whether they accompany the vessels traversing the scleral tissue. The cells are quite numerous in the sclera and corneal conjunctiva and in great abundance in the limbus conjunctivae. The iris is very poorly provided with them; a cell is found here and there in the region toward the posterior chamber. This striking relative deficiency of the iris in vitally staining cells apparently was not noticed by Goldmann¹⁴ who made the most extensive studies of vital staining with reference to internal and external secretions. But the statements of his findings in the eye are so brief that we hardly need discuss this difference in our observations. Assuming that these cells denote the presence of lymph-capillaries, the extreme scarcity of such

channels in an organ which is well supplied with blood-vessels is surprising, for we may admit with some of the best authorities in anatomy that lymph-vessels may be supposed to exist wherever there are blood-vessels. This unaccountable scarcity of vital staining cells in the iris is the more striking because the region which adjoins it is unusually rich in vitally staining cells, namely, the ciliary body and chiefly the ciliary processes. The cells are in proportion more plentiful here than in any other part of the eye. They are arranged along the blood-vessels, from which, however, they are always some distance removed. They are present in all the processes; they are always in abundance and they are always arranged in the same way. When the injections of the staining fluid have been continued for some time these cells are very large and the granules are very coarse; in the iris or sclera they remain small and slender, an observation to which also Schnaudigl calls the attention. This author believes that these cells have an almost dangerous affinity for the staining substance; they are very vulnerable and show the injurious effect of the dye after prolonged contact with the staining fluid. He also believes that this affinity for the dye correlates to specific functions and that these consist perhaps in more than the secretion of the aqueous humor. From the root of the ciliary processes the cells are observed to occur in small number along the subjacent inner layer of the ciliary body; the deeper region, facing the sclera, is scantily supplied with these cells and resembles the iris in this respect. In the choroid, cells are found chiefly in the chorio-capillaris. There are none in the retina. The endo- and perineural tissue contains vitally stained cells. The loose orbital tissue is relatively poor in these cells. The muscles of the eye show the cells in the interfascicular and interfibrillar tissue, generally in the neighborhood of the blood-vessels. They seem to be in closer relationship to the blood-capillaries than, for example, in the ciliary processes; they often seem to spin around the capillaries while these again wind about the muscle fibers. In the lacrimal gland they occur in the interacinous tissue and the connective tissue surrounding the glandular structures. The lids and the nictitating membrane are well supplied with them; they always

occur in the same arrangement and the same distribution. The cartilage is absolutely free from such cells.

If we are to admit the view that these cells represent the endothelium of lymph-capillaries, we recognize that these findings correspond quite well with what we actually know or may reasonably presume concerning the lymph supply of the different parts of the eye.

Until recently our knowledge of the lymphatic system of the eye as of that of the dental region was very limited. I will sum up the most essential anatomical data which enter into the frame of this study.

The most important of recent work on the lymphatics of the eye is that of Most.¹⁵ His results showed, in brief, the following: The conjunctiva of the lids and the eyeball contain very delicate but dense networks of lymph-vessels. At the free border of the lids they pass over into those of the skin of the eyelid. The lymph-vessels from these two networks are divided into superficial and deep ones, chiefly according to whether they arise from the outer skin of the lid or from the conjunctiva; a sharp separation is not possible since both regions communicate with each other. The superficial vessels are apparently finer and less numerous; they course in front of the orbicularis muscle and in the superficial portions of the subcutaneous fatty tissue and only in the neighborhood of their regional glands do they pass into deeper regions. The deeper vessels form many anastomoses in the deep cellular tissue of the lids and then pass on peripherally behind the orbicularis muscle. The superficial as well as the deep vessels are divided into a lateral and a median set; they empty into the submaxillary lymph-glands.

The superficial lateral vessels originate chiefly in the skin of nearly the entire upper lid and about the outer half of the lower lid. Their first and chief regional gland is a typical gland situated superficially in the parotid gland at the level of the external auditory canal. From this gland vessels go to other deeper parotid lymph-glands. Only exceptionally do the superficial lymph-vessels empty directly into the deep nodes. One or two lymph-nodes situated at the lower parotid pole and belonging to

the group of the superficial cervical glands are also to be considered as regional glands, because they may receive direct afferents from those regions of the eye.

The deep lateral vessels arise in the conjunctiva of the upper lid and the outer third of the lower lid. The regional glands, besides the superficial typical parotid lymph-nodes, include one or two nodes deeply embedded within the parotid gland itself.

The superficial median vessels arise chiefly in the skin of the inner half of the lower lid and that of the inner corner of the eye. Their regional gland is one of the submaxillary lymph-glands, especially that situated mesially of the anterior facial vein. The deep median vessels arise chiefly from the conjunctiva of the inner two-thirds and from the region of the caruncula. They form frequent anastomoses in the lid and pass along the anterior facial vein to the submaxillary glands and chiefly to a gland lateral to the one mentioned before. Sometimes this one is also injected. All these lymph-vessels go secondarily to the deep cervical glands situated along the internal jugular vein, at the junction with the facial vein. A direct connection of lymph-vessels of the lids and conjunctiva with these secondary glands could not be demonstrated. Before the vessels of the lids and conjunctiva, and especially the median vessels, enter the parotid and submaxillary lymph-glands they may pass through intermediary lymph-nodes of the face (*lymphoglandulae buccales sive faciales*) situated along the course of the anterior facial vein.

The submaxillary lymph-glands receive also the lymph from the outer vessels of the gingiva of the upper and lower jaw, from the inner vessels of the lower jaw, and from the vessels of the peridental membrane of all teeth. No absolutely definite lines, however, can be drawn with regard to their relation to the different groups of teeth. For there are, on the one hand, variations in the number and location of the lymph-nodes themselves; on the other hand, it not infrequently happens that single lymph-vessels from a definite region pass by the regional node into which all the others enter and empty directly into a remoter lymph-node. Another reason for this irregularity is the fact that the vessels from the gingiva form plexuses in the upper and lower mucosal

fold of the vestibulum oris, from which lymph-vessels pass out into the lymph-glands.

An important path of communication between regions of the eye and the teeth is through the infra-orbital canal with its nerves, arteries, veins, and lymph-vessels. These send branches in either direction. Two small canals, the anterior and median alveolar canals, divide off directly from the infra-orbital canal and are continued as grooves within the wall of the antrum of Highmore. They transmit the corresponding nerves and blood- and lymph-vessels to the premolar, canine, and incisor teeth. The posterior alveolar canals, of which there are two or more, are continued from foramina on the infratemporal surface of the maxillary bone. They transmit the alveolar nerves and vessels to the molar teeth and also to the walls of the antrum. Within the wall of the maxillary bone all these canals form grooves rather than canals. Very little is known yet of the lymph-vessels of the accessory sinuses. Schweitzer¹⁶ states he observed that lymph-vessels from the maxillary sinus passed out of the infra-orbital foramen and entered the submaxillary lymph-glands.

In the endless controversies concerning the identity or difference of tissue spaces and true lymph spaces it has been customary to use the investigations of the cornea of the eye as the chief basis for discussions. The corneal spaces are not recognized now as lymph spaces. These and other spaces, like Tenon's space, the suprachoroidal space, spaces in joints and tendons, the endo- and perilymphatic spaces of the ear have only a remote relationship to the lymph system; their functions differ in every case; frequently they serve only to facilitate gliding motions and displacements necessary in the movements of the eye.

The iris contains spaces filled with fluid, which communicate with the anterior chamber and with the spaces in the ligamentum pectinatum through the furrows or crypts on the anterior surface. These spaces in the iris are regarded as belonging to the lymph system.

Genuine lymph-vessels have not been demonstrated either in the choroid or the sclera. According to Sattler,¹⁷ the veins of the vascular layer of the choroid are surrounded by perivascular

sheaths, lined with endothelial cells. Toward the capillary layer, there exists, he believes, a continuous endothelial membrane which represents the limiting membrane of the vascular layer.

There are no lymph-vessels in the retina.

It has become customary to consider the ciliary body as the main source of the intra-ocular fluid (Leber,¹⁸ Wessely^{19, 20}). Hamburger²¹ ascribes also to the iris an important rôle in the function; in fact, he believes that every part of the eye participates in the secretion and resorption of the fluid. Wessely is of the opinion that it comes nearest to a transudate. It does not contain any substance which is foreign to blood-serum. There is, hence, no reason why we should not consider the process of its secretion as a filtration process. Some difficulties arise from the relatively high salt content and the involved greater osmotic pressure, a property which it shares with the lymph. The most striking difference is no doubt the low albumen content which places it, on the one hand, in a class with the cerebrospinal fluid, the amniotic fluid, and the urine excreted in the glomeruli of the kidney, and, on the other hand, makes it stand in marked contrast to the lymph. Counterpressure to transudation may be the explanation; but we are quite as well justified in supposing that the presence of a special epithelial layer which covers the vessels may be the cause of the retention of the albumen. In the eye, the epithelium of the ciliary processes and the endothelium of the iris may act as such barriers.

Schnaudigl¹³ expresses the view that the vitally staining granular cells in the connective tissue of the ciliary body may be the chief agents in the secretion of the intra-ocular fluid. The epithelial cells covering the ciliary processes remain colorless in injections of trypan blue, an observation which I also made with lithium carmine. It does not seem permissible to me to assume this specific function from the mere fact that these cells have a pronounced affinity for stains. For we must bear in mind that not only do vitally staining cells practically occur throughout the body in the connective tissue, but also that invariably they are larger and more coarsely granular in definite regions of the body, for example, in the pia of the brain, where they occur in patches,

in the choroid plexus, in certain regions of the nasal apparatus. On the other hand, there are cells admittedly endowed with secretory functions, cells other than those within the connective tissue, which also have a pronounced affinity for vital stains (the epithelial cells of the choroid plexus, in the hypophysis, the thyroid gland, the syncytial cells of the placenta, the epithelial cells of the convoluted tubules of the kidney), while other cells of a similar type are not stained by trypan blue or carmine. I am more inclined to believe that, inasmuch as these particular vitally staining cells occur practically everywhere in the connective tissue, they have everywhere the same function to perform and, inasmuch as in some localities they are invariably more intensely stained, they are involved either more intensely in the same process or in another associated function. Along this line of reasoning we may also assume that the function of lymph secretion or lymph resorption is associated with the secretion of a fluid related to lymph, such as the cerebrospinal fluid, the intra-ocular fluid, or even the chyle. From this standpoint the great scarcity and smaller size of vitally staining cells in the iris would speak against the view of some writers that the iris is notably involved in the secretion of the aqueous humor, while the presence of a large number of intensely staining granular cells in the ciliary body support the more generally accepted theory that these are the main source of the intra-ocular fluid. On the other hand, there is nothing in my view of the part which the vitally staining cells play in the lymphatic apparatus that would contradict the view expressed by Hamburger that there is a more active resorption of the fluid by the iris through lymph-channels than the generally assumed venous drainage into the canal of Schlemm. The fluid has a direct entrance into the iris through the crypts and thence into the lymph-vessels. According to my observation, lymph-channels which simply convey lymph have no vitally staining endothelial cells. This might explain the curious fact that there are so few of such cells in the iris, especially in the anterior portion. As to the drainage into the canal of Schlemm, Hamburger states, that the resorption through the spaces of Fontana may also be along perivascular lymph-spaces and not by the blood-vessels.

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PLATE

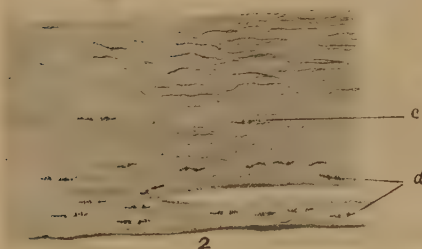
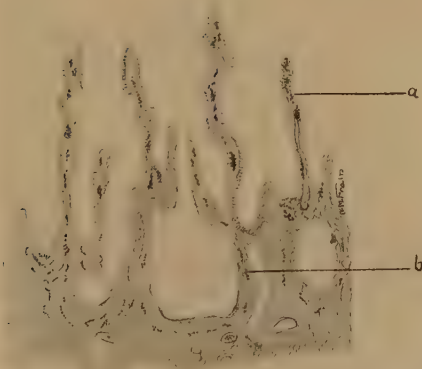
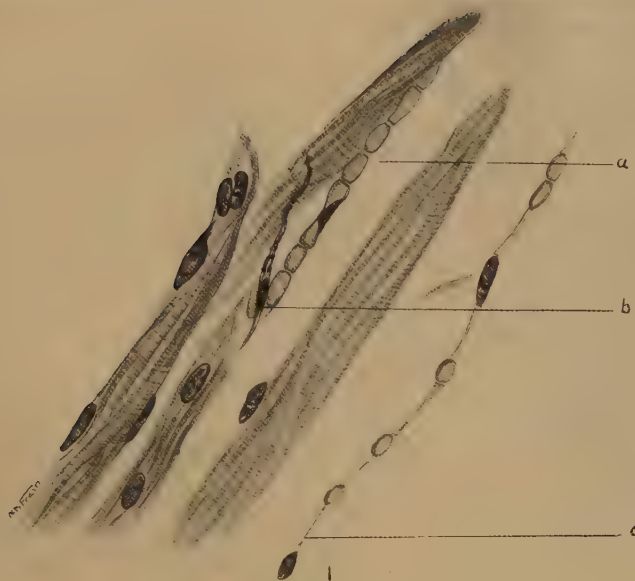
PLATE 1

EXPLANATION OF FIGURES

1 Retrobulbar muscle tissue, stained with hematoxylin. *a*, blood-capillary winding about a muscle fiber; *b*, vitally stained granular endothelial cell, presumably of the lining of a lymph-vessel with collapsed walls; *c*, blood-capillary with two nuclei and separated blood-corpuscles, illustrating how the walls collapse as those of the lymph-capillaries, when no corpuscular elements hold them apart.

2 Cross-section through the ciliary body, sclera, and conjunctiva. Unstained. *a*, large granular endothelial cells in the ciliary processes; *b*, smaller cells at the base of the processes; *c*, fewer slender cells in the outer third of the sclera. There are none in the inner two-thirds of the scleral tissue; *d*, numerous larger cells in the conjunctiva.

3 Longitudinal section of a ciliary process. Stained lightly with hematoxylin. *a*, epithelial cells; *b*, blood-vessels; *c*, large granula cells.



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Contaminación de los cadáveres por el *Saccharomyces cerevisiae*.

El crecimiento de hongos sobre los cadáveres es causa de considerable pérdida de material en los laboratorios anatómicos. El presente trabajo da a conocer la existencia de tal contaminación. Un estudio de los caracteres de los cultivos de dichos hongos, sus propiedades de coloración, morfología y experimentos sobre animales, demuestran que esta "levadura" es una variedad no patógena y saprofítica del *Saccharomyces cerevisiae*. Un estudio de varios germicidas y antisépticos demostró que el crecimiento de estos hongos se impide embalsamando los cadáveres con la siguiente fórmula: Glicerina, 300 cc.; formol, 400 cc.; alcohol, 1000 cc.; fenol, 90 gramos; agua, 400 cc. Primero se usó el bicloruro de mercurio (90 gramos), pero después se omitió su empleo porque forma un coágulo resistente y granular en los vasos sanguíneos, que impide la penetración completa del líquido embalsamador, y, además, por el coste de dicha substancia química. Su presencia en el cadáver no es necesaria para impedir el crecimiento del hongo. Como medida profiláctica paños mojados en la siguiente solución, con los que se envuelven los cuerpos, impiden el crecimiento de la levadura así como la desecación y endurecimiento rápidos de los músculos expuestos. La solución se compone de: Glicerina, 50 cc.; fenol, 2 gramos; alcohol, 50 cc.; agua (que se añadirá) 1000 cc.

Translation by José F. Nonidez
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CONTAMINATION OF CADAVERS BY SACCHAROMYCES CEREVISIAE

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TWO FIGURES

Recently the cadavers in the anatomical laboratories of the University of Illinois, College of Medicine, became covered by a moist, slimy, slightly elevated growth that has caused no small amount of trouble and annoyance. The growth is dirty gray in color, loosely adherent, and does not penetrate the deeper tissues. It has never been noticed upon the unbroken skin of the cadaver; when the skin is removed, however, the growth begins and spreads with great rapidity, making dissection of the specimen out of the question and causing great waste of material.

A quantity of this grayish substance was taken to the bacteriological laboratory for examination. Smears showed a large number of highly refractive, ovoid cells, measuring about 7μ in diameter. In addition to these, there were large numbers of bacteria, especially staphylococci.

It seemed plain that the slimy growth was largely made up of the above-mentioned ovoid cells, and cultures were therefore made in order to isolate and study them in detail.

After several attempts, pure cultures of the organism in question were obtained.

CULTURAL CHARACTERISTICS

Neutral plain agar. After twenty-four hours' incubation at 37°C . small, round, bluish-gray colonies, about the size of a pin-head were seen. Their margins were smooth and regular. After an additional twenty-four hours' incubation at room temperature

these colonies turned white in color, but did not increase in size or number.

Five per cent dextrose agar. Twenty-four-hour cultures showed a growth similar to that on plain agar. After another twenty-four hours at room temperature they were much larger and creamy white in color, becoming confluent in most cases so as to cover the entire surface of the media. The characteristic odor of 'yeast' was noticed.

Plain broth. The growth in plain broth was not profuse. There was a slight flocculent sediment at the end of twenty-four hours. The broth was slightly turbid.

Five per cent dextrose broth. The growth was similar to that in plain broth, but more pronounced; a heavy sediment and the characteristic odor of yeast.

Litmus milk. A marked acid production at the end of forty-eight hours with coagulation; the curd in most cases being completely digested, leaving a whitish turbid whey.

Gelatin stabs. Gelatin-stab cultures showed only a slight growth upon the surface, resembling that on plain agar. No liquefaction.

The organism ferments glucose with the formation of carbon dioxide and alcohol.

STAINING PROPERTIES

The organism stains fairly well with the ordinary dyes and exceptionally well by the Gram method, being strongly Gram-positive (figs. 1 and 2). When stained by Wright's stain, a well-defined blue cell membrane is seen with pale blue mitochondria and numerous vacuoles within.

MORPHOLOGY

The organisms average about 7 μ in diameter and are round to ovoid in form. In a hanging-drop preparation of a forty-eight-hour culture, a highly refractive, non-motile, double-contoured cell is seen in an active state of budding. The budding generally takes place from the long end of the ovoid cells. The younger

cells are small and more rounded in form, while the older cells, from which the budding takes place, are more elongated. There is no tendency to form mycelia.

A pure known culture of *Saccharomyces cerevisiae* was compared with the organism taken from the cadaver, and it was found that in every way the two resembled each other in morphology, staining properties, and in general cultural characteristics.

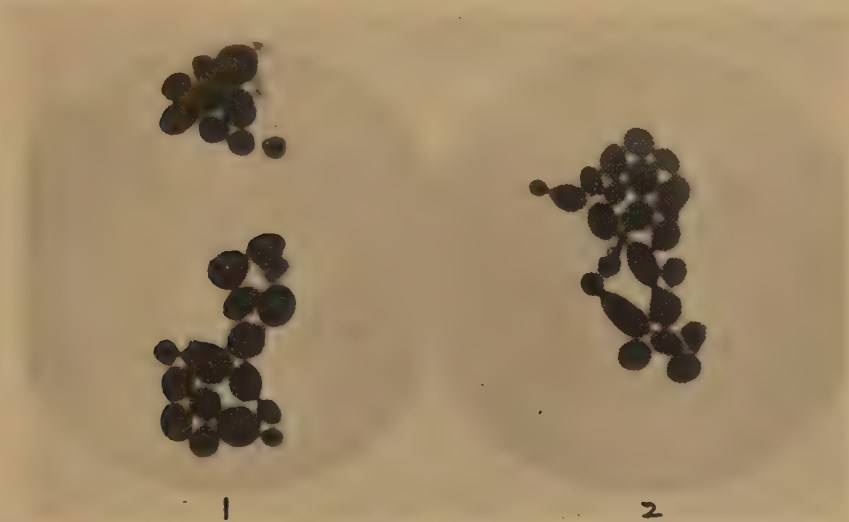


Fig. 1 Strain 'A.' *Saccharomyces cerevisiae* from cadaver. Gram's stain ($\times 1200$).

Fig. 2 Strain 'B.' Known pure culture of *Saccharomyces cerevisiae*. Gram's stain ($\times 1200$).

ANIMAL EXPERIMENTS

White mice, after being inoculated with rather large doses of a normal salt suspension of the organism, showed no ill effects.

An effort was made to reproduce the growth upon animals. Two dead rabbits, with the skin and viscera removed, were immersed in the embalming fluid used for the preparation of the bodies in the anatomical laboratories. This embalming fluid consists of—

Glycerin.....	300 cc.
Formalin.....	400 cc.
Alcohol.....	1000 cc.
Phenol.....	45 grams
Water.....	400 cc.

After a period of one week they were removed and a pure culture of the cadaver organism planted upon one and a pure known culture of *Saccharomyces cerevisiae* planted upon the other. At the end of three days the entire bodies of the two rabbits were similarly covered with a slimy, grayish film. Two days later this growth became a dirty, creamy white and resembled that found upon the cadavers. Thus, it is further evident that the two organisms are alike.

THERMAL DEATH POINT

A series of small test-tubes, each containing 2 cc. of a suspension of the cadaver culture (strain 'A') and a known strain of *Saccharomyces cerevisiae* (strain 'B') were used. At the different degrees of temperature indicated in the table, tubes of each of the two organisms were placed in a water-bath for a period of ten minutes, allowing one minute for the temperature of the tubes to reach that of the water-bath. The tubes were then removed and 5 per cent dextrose-agar slants inoculated and incubated. The results are given in the table. Both organisms were killed at 58°C. for ten minutes, but not at 56°C. for ten minutes.

Because of the apparent identity of the cultural characteristics and staining properties, as well as the results of the animal experiments with the organisms, it is further evident that the contamination of the cadavers is a strain of *Saccharomyces cerevisiae*.

I have been able to find nothing in the literature concerning the contamination of cadavers by *Saccharomyces cerevisiae*. In a personal communication from Dr. Irving Hardesty, of Tulane University, he states that he has had a similar experience with 'molds,' that the mold thrives on formalin-hardened bodies, that alcohol favors its growth, and that carbolic acid will not check it unless the bodies are completely immersed in the carbolic solution.

In order to find some disinfectant for this organism that might be effective in embalming fluids, the following experiments were performed:

The carbohc coefficients for potassium chromate, formalin, and mercuric bichloride were determined according to the method advocated by the U. S. P. H. S. (Hygienic Laboratory Bulletin no. 82) and further described by M. J. Rosenau in his test on "Preventive Medicine and Hygiene." Instead, however, of finding the coefficient with the use of a twenty-four hour culture of typhoid bacillus, forty-eight hour cultures of the two strains of

TABLE 1
Thermal death point

TEMPERATURE (10-MINUTE EXPOSURE)	STRAIN 'A' GROWTH	STRAIN 'B' GROWTH
°C.		
48	Positive	Positive
50	Positive	Positive
52	Positive	Positive
56	Positive	Positive
58	Negative	Negative
62	Negative	Negative
64	Negative	Negative
68	Negative	Negative
70	Negative	Negative
72	Negative	Negative
74	Negative	Negative
78	Negative	Negative

Saccharomyces cerevisiae were used, because the yeast is in its most active state of budding at that time. It was found, by determining the carbohc coefficient, that phenol is the most efficient disinfectant for these yeasts. The action of mercuric bichloride toward these organisms is too inconstant for one to reach any definite conclusion as to its use. Formalin and potassium chromate have too low a coefficient to be of any value.

The prevention of this growth was now attempted by altering the composition of the embalming fluid previously used. A rabbit was embalmed with the following fluid:

Glycerin.....	300 cc.
Formalin.....	400 cc.
Alcohol.....	1000 cc.
Phenol.....	90 grams
Mercuric bichloride.....	90 grams
Water.....	400 cc.

It will be seen that this solution differs from the one previously mentioned in that the phenol is doubled and mercuric bichloride is added. The rabbit was immersed in the same solution for three days, seeded with cultures of both yeasts, and then covered with moist towels. At the end of four days there was no growth. It was considered inadvisable to include mercuric bichloride in the embalming fluid not only because of the extra expense, but because there is a granular coagulation of the blood in the small vessels. This firm, granular coagulum completely obstructs the smaller vessels, thus preventing the thorough penetration of the solution. Other rabbits, embalmed with the same fluid minus the mercuric bichloride, were seeded with both strains of the yeast and incubated for four days. These also showed no growth.

An examination was made of the dust taken from the floor, walls, and tables of the anatomical laboratory. Some of this dust was taken up by means of a sterile cotton swab and 5 per cent dextrose broth and agar inoculated and then incubated for twenty-four hours at room temperature. Many of the samples revealed *Saccharomyces cerevisiae*.

As a prophylactic measure, cloth was soaked with the following solution:

Glycerin.....	50 cc.
Phenol.....	2 grams
Alcohol.....	50 cc.
Water (q. s. ad).....	1000 cc.

and was draped over one-half of the bodies in the laboratory (group A) at the end of each dissection for a period of four months. The other half of the cadavers (group B) served as a control. During these four months none of the bodies of group A was affected, while six of the bodies of group B became covered with the growth.

By applying the above solution upon the embalmed bodies, the specimens are not only protected from the yeast but the glycerin keeps the exposed muscles more soft and pliable.

CONCLUSIONS

Because of the apparent identity of the cultural characteristics, morphology, staining properties, and of the animal experiments mentioned, it is concluded that the organism in question is a saprophytic strain of *Saccharomyces cerevisiae*.

The growth of *Saccharomyces cerevisiae* upon anatomical specimens renders them useless, thereby causing great waste of material.

Phenol is the most efficient disinfectant for this particular strain of yeast.

The contamination can be prevented by using the embalming fluids and the prophylactic measures mentioned.

The use of mercuric bichloride in embalming fluids is not practical; first, because it forms a firm granular coagulum of blood in the vessels, thus preventing the complete penetration of the fluid, and, second, because of the expense of the chemical. The prophylactic measures indicated not only protect the cadavers from the *Saccharomyces cerevisiae*, but prevent rapid drying and hardening of the exposed muscles.

Abstracted by E. D. Congdon, author.
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Simultaneous occurrence of very small sphenoid and frontal
sinuses.

Because of the uncertainty as to the reason for failure or incompleteness of sinus development, the present almost unique instance of very rudimentary condition of four sinuses merits description. The sphenoid sinuses were symmetrical in form and position. They were about 4 mm. in sagittal and 14 mm. in craniocaudal diameter. A lateral extension of the cavity brought each into series with the corresponding posterior ethmoid cells. The ostium of the left sinus was so far forward and so lateral as to almost justify the interpretation that it was an ethmoid cell. The ostium region on the other side was destroyed. The cavity interpreted as the left frontal sinus was so small that it is not certain that it extended beyond the ethmoid bone. There was no especial condensation of compact bone to warrant the supposition that the sinuses may have been hindered in their development by infantile disease. It is possible that the sphenoid sinuses are to be grouped with others previously described by the writer which were apparently unable to expand through material of the concha-presphenoid fusion plane. No compensation for the loss of these cavities was noticeable in the size of the other sinuses.

SIMULTANEOUS OCCURRENCE OF VERY SMALL SPHENOID AND FRONTAL SINUSES

E. D. CONGDON

TWO FIGURES

A few very small sphenoid sinuses have been recorded, and complete absence has been claimed by several observers. Incomplete development and absence of frontal sinuses are both rather frequent. Only one previous record was found of the slight development of sinuses of two types in the same individual. This also had to do with the frontal and sphenoid cavities. They were described by Wertheim ('01) in an eight-year-old child. The observation was made for a sufficiently early stage of development to admit of the possibility that the deficiency would have been made good to a considerable degree before adult life.

The explanations which have been advanced for the absence and incomplete development of the sinuses are at present supported by little evidence. Information regarding the paranasal region needs to be collected in these cases if any explanation is to become more than a hypothesis. Although it is especially desirable that this be obtained for foetal and infantile specimens, since observations on such material will of necessity be rather infrequent, the conditions surrounding absence or incomplete development of adult sinuses should be examined for whatever information it can afford.

The rudimentary sinuses were found in the course of dissection and were preserved with the mucoperiosteum nearly intact. The subject was an adult male apparently of European parentage. The small spherical cavities were symmetrically developed and extended to the orbit behind the last posterior ethmoid cell (fig. 1). The anteroposterior diameter of the portion lying within the area usually ascribed to the sphenoid was 4 mm. and its height 14 mm. upon the right and 12 mm. upon the left side.

The ostium of the left sinus opened backward, although it was so far lateral as to be little posterior to the nearest ethmoid cell. Were it not for the position of the aperture, the sinus could as well be classified as a posterior ethmoid cell with a recess in the sphenoid bone, because the part of the cavity in series with the ethmoid cells has a position frequently occupied by one of them, and the most posterior ethmoid cell also not rarely invades the supero-anterior part of the sphenoid where the median portions of these sinuses were located.



Fig. 1 Parasagittal diagrammatic drawing through left sphenoid sinus (*a*). Three posterior ethmoid cells as (*b*) represented by dash lines. A fourth, the most posterior which had been opened in dissection outlined in an unbroken line. Above it the aperture of the sphenoid sinus also shown by an unbroken line. $\times \frac{1}{2}$.

The portion of the wall of the right sphenoid sinus corresponding to the aperture of the left is not perforated and no communication of the sinus on this side with the nasal cavity occurs elsewhere. A saw cut has destroyed that part of the wall lying a little more medially. Either the aperture must have been situated in this region then or the sinus lacked an outlet. There has been considerable discussion as to whether this second alternative ever occurs. Some authors categorically deny that a sinus can originate without an opening, since they believe sinus formation is always by the out-pocketing of the nasal cavity. Zuckerkandl ('93) states that he has seen two sphenoid sinuses

without apertures in their bony walls. No other record of the lack of opening to the osseous wall of a sphenoid sinus was found. Evidently its absence is very rare, although closure of the aperture by the swelling of the mucosa is frequent. For this reason and because the closely similar companion sinus had an opening, it is very probable that its aperture was destroyed by the saw.



Fig. 2 Right frontal sinus (a). $\times 1$.

The more rudimentary of the two frontal sinuses is shown in figure 2. There is a marked difference in the frequencies of absence of the frontal sinus as given by various authors. Onodi ('11) places it as high as 20 per cent, while Boege ('02) finds it to be only 4.9 per cent. Much of this discrepancy is probably due to different conceptions of what constitutes the earliest developmental stage of a frontal sinus as contrasted with a beginning ethmoid cell. The recess (fig. 2, a) is here regarded as a frontal sinus because it is already separated by a ridge from another division of the frontal recess and is in the proper position

to enlarge directly into the frontal bone. It is the passage into the frontal bone upon which the application of the term frontal to a sinus should depend, but it is usually not practicable, even if it is not impossible, to determine whether small out-pocketings of the frontal recess have passed beyond the confines of the ethmoid bone or not.

No peculiarities were observed in the other paranasal sinuses which could aid in finding the reason for the rudimentary condition of the frontal and sphenoid sinuses. The spongy bone surrounding the four sinuses was somewhat more dense than the average. It may be, therefore, that foetal or infantile disease may have brought about a condition which interfered with the enlargement of the sinuses. Onodi ('11) and Wertheim ('01) have brought together some evidence of such an occurrence. The condensation of the spongy bone was not extreme, and, since there was no atrophy of the mucosa, the argument for early disease is not convincing. Furthermore, it would be surprising that sinuses at opposite ends of the nasal cavity should be affected while the maxillary and ethmoid sinuses opening at intermediate positions are normally developed.

The explanation first suggested by Toldt ('83) for the origin of the bony plates in the sphenoid sinus and further elaborated by Cope ('17) and the writer ('19) may possibly be applicable also to the retardation of the sphenoid sinuses. Toldt regarded the planes and ridges as the remnant of material at the plane of fusion of the adjacent ossification centers of the sphenoid sinus which was able to resist the absorptive action of the periosteum during the enlargement of the sinus.

Seven sphenoid sinuses out of two hundred and forty-two were found by the writer ('19) whose posterior walls corresponded in position and direction with the usual plane of fusion of conchal and presphenoid centers. This led to the suggestion that resistant material had prevented the extension of the sinus backward. The two rudimentary sinuses here under discussion have posterior walls lying more anteriorly and somewhat more transversely than the usual position of the plane. It may be that in this instance a plane situated especially far anteriorly put an early stop to the backward extension of the sinuses.

The incomplete development of the two pairs of sinuses in the same individual is suggestive of a correlation between the development of the two types. The interrelation of form and size of adult sinuses seems to show that alternative correlation is a common feature of sinus development when one of two adjacent sinuses succeeds in preempting space originally open to both and thus brings about the underdevelopment of its neighbor. The suggestion has also been made that as an adaptation to keep the total sinus space up to the usual amount the underdevelopment of some sinuses might be correlated with an unusually extensive growth of others through some unknown mechanism. As far as could be found, there is no evidence for the occurrence of a growth response of this nature. If there is a correlation which explains the concurrent retardation of development of the four sinuses in the specimen which has been described, it differs in type from the relationship just referred to in that the sinuses all vary from the norm in the same direction. The retardation or absence of two frontal sinuses is so often bilateral as to be probably correlated. Less data are at hand for sphenoid sinuses, though a certain degree of correlation is probable. The retardation of development of frontal and sphenoid sinuses in the same head is so rare that its coexistence in the two types is probably a matter of chance.

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Abstracted by E. D. Congdon, author.
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Anomalous fibrous cords in the hand and the phylogeny of the
flexor digitorum sublimis tendon.

The fibrous cords are evidently remnants of the ancestral short flexor muscles of the hand which are normally represented by the distal part of the flexor digitorum sublimis tendons, according to Eisler's theory. They were attached proximally on the radial sides of the bases of the proximal phalanges of the fourth and fifth digits and extended distally to bifurcate like the flexor digitorum sublimis tendons and insert on either side of the volar surface of the middle phalanx. The coexistence of the cores with normal flexor digitorum sublimis tendons apparently either contradicts this interpretation or disproves the theory. Also Bardeleben and Kajava state that the flexor digitorum sublimis tendon may exist side by side with the short musculature in certain mammals, and Fromont describes an anomaly in the human hand showing this condition. Since there are compelling reasons both from comparative anatomy and embryology for Eisler's theory, it is probable that in these apparently contradictory instances the rudiments of the short flexors split to go only in part to the sublimis tendon, while the rest was retained to form more or less perfect short superficial flexor muscles.

ANOMALOUS FIBROUS CORDS IN THE HAND AND THE PHYLOGENY OF THE FLEXOR DIGITORUM SUBLIMIS TENDON

E. D. CONGDON

TWO FIGURES

Tendon-like cords were found in one hand of an aged male subject during the course of dissection by Mr. A. F. Warren. They lie upon the volar sides of the fourth and fifth fingers of the right hand and are closely similar in form and position (fig. 1). Each extends distally from an attachment on the radial side of the base of the proximal phalanx to the volar surface of the vaginal ligaments and there bifurcates. The slips thus formed pass to the opposite sides of the middle phalanx to insert into the vaginal ligament the adjacent fascia and the border of the dorsal extensor aponeurosis. Although of a somewhat less compact structure than a tendon, they can by no means be described as mere condensations of fascia. They did not bring about any marked flexion of the digits in the cadaver, and probably did not hamper movement during life.

The muscles to which the cords seem related are the short superficial digital flexors of amphibia, reptiles, and mammals. These take origin usually upon or in the volar fascia and have insertion in part at least by a pair of slips upon the sides of the metacarpo-phalangeal joint or more distally. The cords differ from the muscles in the position of their proximal ends. Instead of passing to the palmar aponeurosis along the mid-line of the digit they are deflected to the side of the base of the proximal phalanx. The dissimilarity is not great, however, because the cords are in continuity on the phalangeal bases with slips of insertion of the palmar aponeurosis. The relationship of the cords are not like those of the lumbricales or interossei, nor are either of these muscles abnormal or lacking.

The presence of ten short digital flexors in urodele amphibians, in monotremes, and marsupials is generally accepted as sufficient reason for regarding the structures as an ancestral muscle for man and other mammals possessing the flexor digitorum sublimis muscle. As will be seen Testut and Fromont have also described the primitive short superficial flexors in the adult human hand. It can be accepted with a large degree of confidence then that the anomalies in question are actual short superficial flexor remnants.

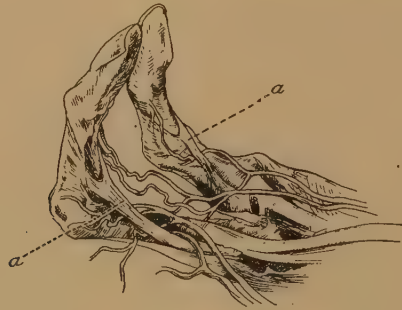


Fig. 1 Hand (after Fromont, with parts omitted) showing abnormal digital muscles. *a.a*, tendon of flexor digitorum sublimis upon which are inserted muscles (*c.c*), interpreted here as short superficial digital flexors; *b.b*, muscles interpreted as short superficial digital flexors taking the place of tendons of flexor digitorum sublimis. $\times \frac{1}{2}$.

The flexor digitorum sublimis muscles of man and many mammals said to arise in part from the short superficial flexor muscles lie in large part within the fore arm, but send their tendons through the palm to the digits. Here they bifurcate to insert on either side of the second phalanx. The flexor digitorum profundus, a companion muscle, whose muscle belly is also in the arm, inserts on the distal phalanges by tendons which pass between the bifurcations of the sublimis insertion. Eisler ('95) suggested that the terminal portion of the sublimis tendon with its bifurcated insertion might be nothing else than a degenerated superficial flexor muscle which after having changed completely to tendon had come, by means of its attachment to the palmar

aponeurosis, to be continuous with a part of the fore arm flexor mass which earlier inserted on the palmar aponeurosis.

McMurrich's careful study of the flexor muscles of amphibians, reptiles, and mammals ('03) gave confirmation and amplification to Eisler's suggestion. It received support of another kind when Gräfenberg ('05) found that a short flexor musculature in the hand of the human embryo connected with a fore arm mass to form a flexor sublimis.

With this view of the origin of the flexor digitorum sublimis muscle it is not to be expected that any mammalian finger will possess at the same time one of its tendons and a short superficial flexor muscle. Kajava ('11) who has examined the digital flexor musculature of monotremes and eleven species of marsupials found, as did McMurrich for other animals, that the two never occurred together in the same digit. Yet Kajava states that there are certain insectivora and carnivora which do possess both the flexor superficialis brevis and the sublimis; Bardeleben ('90) much earlier made a like claim for Hyrax and, according to Eisler (95), for Paradoxurus.

References by two authors to aberrant muscles of the human hand related to the anomaly here described bring confirmation to the theory of end-to-end fusion for the sublimis, but at the same time in part offer difficulties similar to those found by Kajava and Bardeleben. Testut is quoted by Kajava from a work which was not accessible as giving instances of the occurrence of a short flexor in the human hand for the little finger which had replaced the corresponding sublimis tendon.

Fromont found a similar displacement of the flexor sublimis in two digits of the hand. His figure is copied here (fig. 2b). A better confirmation of the theory of end-to-end fusion by a reappearance of the primitive structures could scarcely be desired. The condition of the musculature of two other digits were found however to be more involved, the flexor sublimis was present in each of them, but there were also other slender muscle bellies taking origin from the transverse carpal ligament, and inserting on the sublimis tendons (fig. 2a). The conclusion seems necessary that in these two digits part of the embryonic

rudiment derived from the ancestral short flexor have given rise to the corresponding muscles in the adult. The relationships and origin of these slender muscles are also like those of the two larger short superficial flexors. Fromont terms the two of the four short muscles which insert on the sublimis tendons superficial lumbricals, but likelihood of identity with lumbricals is excluded by their relationships and by the presence of almost normal lumbricals in the usual position in the digits to which they are related.

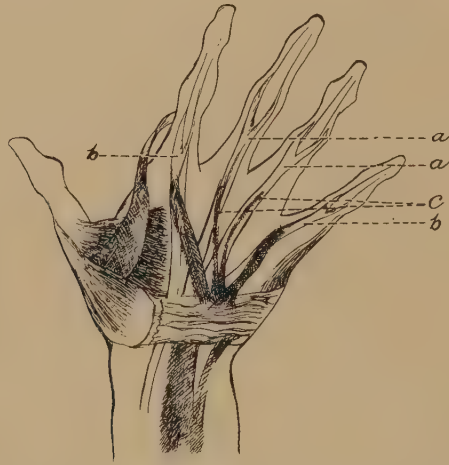


Fig. 2 Fourth and fifth digits of left hand with tendinous cords (*a.a'*) apparently representing remnants of short superficial digital flexors. $\times \frac{1}{2}$.

It has been seen that the instances of abnormal human muscular development described by Testut, Fromont, and the writer confirm the comparative anatomical evidence taken from a wide field by Eisler, McMurrich, and Kajava for the theory of end-to-end fusion to the extent that they reveal a tendency toward the formation of short superficial digital flexors in man. But at the same time the anomalies of Fromont and the writer present a difficulty for the theory in the simultaneous occurrence of the short superficial flexors and the tendons which are supposed to arise from them. Observations of a like condition in the

normal structure of a few other mammals have already been referred to. A possible explanation of this contradiction is that when muscle and tendon appear together, the short flexor rudiment divided at an early developmental period to give rise to both the muscle and the tendon. The supposition that there were paired short superficial flexors in the human ancestry as in some other mammals and that their rudiments give origin one to the muscle and one to the tendon is not probable because of the rarity of the anomaly.

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Acquired skeletal deformities in a young fowl.

A young cockerel reared in an incubator till about three months of age showed marked skeletal deformities which were in part mechanical effects of confinement under a roof with which the bird gradually came in contact as it increased in height. The dorsoventral thoracic diameter was reduced a half. The trunk anterior and posterior to the interacetabular line was bent downward. Apparently the down thrust of the neck against the thorax, due to the striking of the head against the roof, together with the downward pull of the leg muscles upon the posterior portion of the trunk in the effort to keep the body from falling forward were responsible for the bend. There was marked underdevelopment and further deformity of the trunk skeleton. The cervical vertebral column approached adult size, but was retarded in differentiation. The wattles, comb, and beak showed a differentiation typical of a larger cockerel. The gross appearance of the trunk skeleton suggested that the cockerel may have had rickets. No microscopic examination was made. The only indication of poor health which was noted was a ruffling of the plumage for a few days before the animal was killed.

ACQUIRED SKELETAL DEFORMITIES IN A YOUNG FOWL

E. D. CONGDON

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SIX FIGURES

Two young cockerels reared in an incubator showed skeletal deformities approaching in degree the effects of a severe case of human rachitis. Although the influence of mechanical conditions upon the form of the mammalian and especially the human osseous system has long been studied, no descriptions were found in the literature of marked deformities in the domestic fowl or any other bird.

At the time when it was noticed that the chicks had been kept too long in the incubator, their backs were already in contact with the ceiling. As they grew, their heads must have been gradually forced to a lower level relative to the rest of the body.

The cockerels evidenced poor health by a ruffling of their plumage (fig. 1), and they were somewhat sluggish in their movements. There is little doubt that the direct mechanical effects due to unusual posture and contact of the head with the roof were complicated by the influence of the other unfavorable conditions, such as high temperature and lack of exercise. It may be that the slight thickening at costochondral junctions and at the posterior ends of the uncinates, the bending of certain bones and other disturbances of growth, which will be described, are due in part to rickets and osteomalacia. Insufficient attention was given to the question before the skeleton was cleaned to answer the question. Tripier¹ tried the effect of diet with low protein content and containing little earth salts upon two young pullets, and described a change in the physical properties of their

¹ Arch. de Physiol. norm. et pathol. (2) 1, 1874.

bones. He did not mention, however, any change in skeletal proportions or in the shape of the individual bones.

The larger and more deformed of the two fowl was used for a detailed examination of the skeleton. Two cockerels were chosen for comparison, one of these showed less maturity than the abnormal bird in comb, wattles, and bill, but was of nearly the same length and height. The other was chosen because the comb, wattles, and bill indicated an equal maturity. It was much larger than the abnormal fowl, though it was of average size in comparison with other normal cockerels in the same stage of development. The controls and deformed bird were all White Leghorn stock of approximately pure breed.

Figures 2 to 6 show the abnormal and the smaller control birds under equal magnification. The trunk of the abnormal cockerel is the smaller, although, as will be later seen, it would probably have been as large or larger had it developed normally. Some features of its deformity come out strikingly in the profile view with the trunk musculature in position (figs. 2 and 3). The thoracic region has a dorsal and a ventral diameter about half that of the smaller control. The posterior portion of the trunk is also somewhat smaller. A comparison of figures 2 and 4 shows that incomplete development of the breast muscle and sternal keel play a considerable part in the thoracic reduction, though the body cavity in this region is also disproportionately small in cross-section in comparison with the parts external to the trunk.

The chief skeletal malformation which can be readily traced to a mechanical cause consists of a bending downward of the anterior and posterior portions of the trunk, so that their longitudinal axes meet at a slight angle at a transverse plane passing through the hip-joint. The pelvic bones are correspondingly bent at their acetabuli and the sternum at the junction of the cartilaginous and bony portions of the keel. This condition evidently developed as an effect of the frequent down thrust of head and neck upon the thorax, when the head came in contact with the roof as the chicken tried to assume an erect posture. To retain the balance of the body upon the legs at the acetabuli,



Fig. 1 Abnormal cockerel

Fig. 2 Abnormal cockerel

Fig. 3 Younger control cockerel. Magnification the same as in figure 2

Fig. 4 Abnormal cockerel.

when the downward impulse was communicated by the neck to the thorax, the musculature from the legs to the part of the pelvis posterior to the acetabular joints must have contracted with more than ordinary vigor. The two unusually powerful downward forces acting at opposite ends of the trunk resulted in the bending at the interacetabular transverse plane.

The trunk skeleton shows abnormalities throughout that may not be so directly connected with mechanical influences as is the bending of the trunk. The ribs and uncinates are thicker relative to their length than in the control birds. The ends of the costal and sternal ribs, which articulate with one another, and the posterior ends of the uncinates are enlarged. The disproportion of the trunk relative to the neck is shown in the vertebral column by a decrease in size of the successive dorsal vertebrae posterior to the second, in place of the usual increase in their dimensions.

The ossa coxae are not only bent, but are narrower than usual in conformity with the diminished diameter of the entire trunk relative to its length. The bend in the body of the sternum has already been mentioned. Its bony keel is of only half the usual dorsoventral extent at its posterior end, and decreases to an inconsiderable ridge anteriorly. The reduction of the keel is probably due in large part to the direct effect of striking the breast against the bottom of the incubator, when as frequently happened, the down thrust of the neck at the thorax caused the animal to topple forward after pushing its head against the roof. It is not probable that underdevelopment of the breast muscle had much, if anything, to do with lack of development of the keel, because other bones associated with these muscles including the coracoid furcula and body of the sternum, if of less than the usual size, are certainly much nearer to the norm than is the keel. The furcula which extends downward from the superior extremity of the coracoid to the antero-inferior angle of the keel has undergone a reduction in length corresponding to the decrease in the dorsoventral extent of the keel.

There are details in the form of the skull which may be due to the repeated striking and pressure of the head against the roof. It should be stated, however, that these do not greatly exceed in amount the normal variation as shown in the skulls of four other cockerels of about the same age. The frontal region of the skull seems to have been pushed slightly forward and down (fig. 6). The wedge-shaped projection of the cranial cavity lying between the upper and posterior portions of the orbits is enlarged at their expense, so that the orbital processes of the frontal bone are unusually conspicuous in a lateral view of the skull. The anterosuperior orbital region which usually has a nearly straight edge is convex and flares upward, as though the eyeball had been pushed forward against it. A protrusion of the eyeball was not looked for while the animal was alive and it was not noticed. In the photographs of figure 2 and 4 it appears to be present. The comb is bent over as if from frequent contact with the roof, yet its deformity cannot be assigned to this cause with certainty, because lopped combs are not rare among White Leghorns.

Other gross malformations of the osseous system not directly traceable to the effects of pressure of the head against the roof manifest themselves both in the form and in the size of the bones. The ribs, uncinates, coracoid, furcula, and cervical vertebrae are thicker and more rounded than in the controls. The pelvic bones and sternum are so irregular in form that they mask any abnormality of a like nature, which may have been present. The surface markings of scapula, coracoid, furcula, sternum, cervical vertebrae, ribs, and uncinates are less sharply defined than in the control skeletons. The characteristics of form both as regards general outline and detail consist in a retention of an earlier developmental condition modified perhaps by other pathological characters.

Various parts of the skeleton show irregularities in relative volume, some of which have been already mentioned. Though the retardation of the trunk is so marked that it can scarcely be questioned, the less marked differences of relative size in



Fig. 5 Younger control cockerel. Magnification the same as in figure 4
Fig. 6 A. Skull and a portion of cervical vertebral column of younger control cockerel. B. Skull and upper part of cervical vertebral column of abnormal cockerel.

other regions make it difficult to decide which if any of these have normal measurements. The wattles, comb, and bill indicate maturity equal to the older control bird, whose body is twice as large as that of the abnormal cockerel, and was chosen from a number of equal maturity as representing their average size. Since the skull of the deformed bird appears to be normal except for the deformity due to pressure against the roof and is of almost the same length as the control, it may be the birds would have been of equal size as well as maturity, had conditions been normal.

The measurements of the skeleton of the extremity are unfortunately limited to the femur and the coracoid. Both agree closely in length with the smaller control. The appearance of the extremities in figures 2 and 3 confirm this view. The only careful observations of the bone form in these regions were upon the tibiofemoral joint. Here no retardation of development could be noticed.

Comparative measurements of abnormal cockerel, large and small control and rooster

	POSTERIOR END OF OS COXAE TO ANTERIOR END OF 1ST THORACIC VERTEBRA	LENGTH OF SKULL AND BILL	LENGTH OF FEMUR MEASURED ALONG DIAPHYSEAL AXIS	AVERAGE MEASURE- MENTS OF ENTIRE CERVICAL VERTE- BRAL COLUMN		
				Length of cen- trum	Smallest width of centrum	Interval between outer borders of articular pro- cesses
	cm.	cm.	cm.	cm.	cm.	cm.
Abnormal cockerel.....	11.5	6.7	6.7	0.98	0.62	1.24
Younger control (10 months old).	12.0	6.5	6.7	0.91	0.54	1.15
Older control (13 months old)....	14.0	6.8	10.1	0.93	0.54	1.10
Rooster.....	20.0	8.0	13.6	1.27	0.61	1.49

The cervical column has plainly undergone an excessive development in volume, since, as seen in the accompanying table, it is not only larger than the older control in three measurements which were chosen, but it even slightly exceeds a rooster in the minimum transverse diameter of its centrum. The upper vertebrae are especially large and the atlas largest of all (fig. 6.) These facts together with the correspondence, of the limb skeleton in

length with the smaller fowl and its lack of abnormal characters lend some support to the view that the younger control may represent the true size of the deformed bird, had it developed normally and that there has been an overgrowth of skull as well as cervical vertebral column. The less sharply sculptured surface and the more massive form is found in the cervical column, which has been frequently described in other instances of overgrowth. The skull did not show a similar condition, but its comparative freedom from surface elevations would prevent easy recognition of a slight deficiency in this respect.

Abstracted by Francis Marsh Baldwin, author.
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Notes on the branches of the aorta (*arcus aortae*) and the subclavian artery of the rabbit.

Although the usual number of blood-vessels arising from the aorta in the rabbit is two—a so-called innominate or brachiocephalic and the left subclavian arteries—the variation from this condition herein described indicates the possibility of a considerable departure. Of 106 specimens, about 20 per cent differed from what is usually considered normal, either in respect to the aortic vessels or the subclavian arteries of either side. In one individual a single vessel leaves the arch of the aorta, and after passing forward subsequently successively subdivided to form the left subclavian, the left common carotid, and the innominate or brachiocephalic arteries. When three vessels originate on the arch, they are usually the innominate and the two carotids, although in one case the vertebral of one side contributed to this arrangement in the place of a carotid. Several individuals show conditions suggestive of four vessels, comprising the two carotids, the left vertebral and left subclavian. The order and sequential differences of vessels from the subclavian arteries of each side are noted.

NOTES ON THE BRANCHES OF THE AORTA (ARCUS AORTAE) AND THE SUBCLAVIAN ARTERY OF THE RABBIT

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ELEVEN FIGURES (ONE PLATE)

Bensley,¹ in his Practical Anatomy of the Rabbit (p. 365), in discussing the blood-vessels of the thorax, describes the arch of the aorta as "beginning at the base of the heart, passes forward, and then describing a curve, in the course of which it lies slightly to the left of the median plane, turns backward along the ventral surfaces of the bodies of the thoracic vertebrae. With the exception of the coronary arteries the first branches are the large paired vessels arising from the anterior wall. They comprise the common carotid and subclavian arteries. On the right side the carotid and subclavian arise from a short common trunk, the innominate artery. The left common carotid arises immediately to the left of this vessel or from its base. The subclavian artery (a. subclavia) is the first portion of the artery of the anterior limb. It passes from its point of origin laterad to the anterior margin of the first rib, where it is replaced by the axillary artery. Near its point of origin, it gives off several branches, the relations of which are subject to considerable variation."

The large paired vessels referred to above is not exact and leads to confusion, since even in the usual condition it applies to neither the right and left common carotid arteries, nor the paired subclavian arteries, but to an innominate artery on the right side, and the left subclavian artery on the other. That the left common carotid artery usually arises immediately to the left

of the base of the innominate is perhaps correct, although in by far the greater number of rabbits dissected the origin of this vessel is well up on the mesal side of the innominate. In cases where the left common carotid artery arises to the left of the innominate, there would be three vessels arising from the cephalic curve of the aorta and not two (a pair) as above described, a condition normally found in the human. With reference to the subclavian arteries, the statement as to their branches being subject to considerable variation, is correct, but it seems important that the point should also be made, that great differences occur in these vessels on the right and left sides in the same animal.

Again, Parker and Haswell² describe correctly the relation of these vessels as they occur in the majority of cases, but the figure shown (p. 465) represents the condition in an abnormal individual, where the left common carotid artery originates as a branch from the arch of the aorta, and thus constitutes the third vessel from the arch, the innominate and the left subclavian being the other two. Since these discrepancies exist in the descriptions of the blood-vessels of the region in the various texts, and in view of the variability of both the arteries given off by the arch of the aorta, and their subsequent subdivisions, especially those of the subclavian, it seems of sufficient interest to record their frequency and extent. Accordingly, the following description is based upon the study of over one hundred specimens. Such records, of course, have no immediate practical value from the surgical or pathological sides, but from the educational considerations, especially from the standpoint of comparative anatomy they are rather important. No doubt the variations which are described below are to be explained in part by the persistence of foetal conditions, or in some cases by abnormalities of the vessels themselves, or to the development of extrinsic parts in their immediate region. Many of the changes brought about are probably due to different modes of transformation of the primary vessels of the branchial arches, especially the fourth, since the aorta as well as the pulmonary artery are derivatives of this arch. Again, it is well known that the heart itself originally develops high up in the neck region of mammals, and is

gradually shifted downward, so that this gradual shifting might account for some of the variations noted.

Of one hundred and six rabbits dissected* nineteen individuals showed marked variations from the usual condition, either in the branches from the aorta, or in respect to the subclavian and its branches in either side. There were others (fifteen) which showed minor variations, but which could easily be placed in some of those showing marked variations, so that their condition is represented, partially at least, in some one or in a composite of the subjoined figures.

In what may be termed the usual condition, the aorta (fig. 1, *A*), after giving off the coronary arteries close to its junction with the left ventricle, passes cephalad a short distance, and then describes a curve of a half circle and passes down the back, a little to the left of the ventral vertebrae. From the cephalic curve (arch) a comparatively large innominate or brachiocephalic artery extends upward and a little to the right and soon bifurcates, forming the left common carotid artery which passes immediately across the trachea to the left side of the neck, and a common trunk which gives rise to the right subclavian and the right common carotid arteries. A second branch from the curve of the aorta is the left subclavian artery which passes laterad and forward to branch in various ways. Usually on this side the superior intercostal (costocervical) (fig. 1, *I*) is the first branch to be given off, and passes caudomedial. Just distal in close juncture with the superior intercostal artery is the internal mammary artery, while just opposite arises the vertebral artery. Distally the subclavian artery soon divides into the transverse scapular (*T*) and the axillary (*X*) arteries. On the right side the superior intercostal and mammary arteries arise from a common trunk, as also do the vertebral and transverse scapular arteries just opposite to them. The axillary artery passes to the region of the forearm. In some cases the superficial cervical artery branches from the subclavian, but usually it is a branch of the transverse artery of either side.

* My thanks are due Mr. Ralph L. Parker, my assistant, for aid in dissection.

VARIATIONS OF THE SUBCLAVIAN ARTERY OF THE LEFT SIDE

A number of interesting variations are noted in the order and sequential relationships of the various vessels arising from the left subclavian. Frequently the arteries originating from the subclavian artery in close proximity to each other so that a veritable corona of the vessels is formed. In some cases, as shown in figures 6 and 11, this takes place at quite a distance from the arch of the aorta, and can be called the long corona type, while in others, typified in figures 9 and 10 and perhaps less conspicuously in figure 8, the corona formation is closely approximated to the aortic arch. Where the corona is formed, the usual order of the vessels may be described as normal, i.e., beginning with the vertebral artery originating on the cephalomesal surface of the subclavian, the transverse scapular, axillary, mammary, and intercostal arteries followed in the cycle clockwise. In one specimen an interesting departure is noted, in that the intercostal artery (fig. 6, *I*) takes its origin from the vertebral so that there is formed in this case a very short innominate with the vertebral artery. A number of cases are observed where the intercostal and mammary arteries formed a short innominate in common as is shown in figures 4 and 7. In one rabbit (fig. 3 *V*) the vertebral artery of this side branches from the cephalic surface of the arch of the aorta at about its junction with the subclavian artery, and in this case it is comparatively a much larger vessel than normal. In this specimen also the transverse scapular and mammary arteries have their origin some distance cephalad, and the interval between the intercostal and mammary arteries is very noticeable. In no case is there found an innominate formed by the left subclavian and the left common carotid arteries, which of course is the typical avian condition, and which has been described to occur in most apes, and somewhat more rarely has been noted in the human. In three cases, however, varying in degrees, as shown in figures 6, 8, and 10, the left common carotid artery is a separate branch from the arch of the aorta, and in these the condition closely simulates the normal condition found in the human. In one in-

stance the points of origin of the vertebral and the transverse scapular arteries are interchanged, as shown in figure 2, and in another, figure 5, the vertebral artery arises from the laterocaudal surface of the subclavian in the same manner but distal to the intercostal and mammary arteries, and then turns mesal to enter the transverse foramina of the cervical vertebrae. In the last specimen also a number of excessory blood-vessels are noted, some of which parallel the mammary, others the intercostal arteries.

THE SUBCLAVIAN ARTERY OF THE RIGHT SIDE

The blood-vessels of this side which take their origin from the subclavian artery seem less variable in their relationships than those just described. There is the formation of what may be termed a corona in several instances, but this is with but one exception formed relatively close to the innominate, or to that portion close to the bifurcation of the innominate which forms the subclavian and right carotid arteries. Such a condition is typically shown in figure 5, where the vessels spread out in fan-shape formation about the subclavian. In one instance, the vertebral artery (fig. 2, *V*) originates well cephalad and on the lateral surface of the right common carotid artery, so that its displacement from its usual position is rather striking. As regards the interrelation of the intercostal and internal mammary arteries, all sorts of gradations of intervals exist from the formation of a conspicuous elongated innominate, as is indicated in figure 3, or a much-reduced innominate, as shown in figure 11, to the more or less widely separated intervals, as represented in figures 8 and 9. The intercostal artery in the last case is really a branch of the innominate, and has no connection with the subclavian. Usually the superficial cervical artery of this side as in the normal condition is a branch of the transverse scapular artery, but in two cases it is greatly displaced; one originating from the subclavian (fig. 3) and another curiously entering the common junction of the intercostal-mammary vessels, as shown in figure 10. In one case the transverse scapular artery originates as a branch of the vertebral well cephalad of the latter's

junction with the subclavian, as in figure 8, although in two other specimens this condition is barely suggested in the close proximity of the origins of the two vessels, as in figure 9.

The manner of branching of the two carotid arteries from the innominate is of interest, although not more variable than might be expected. In the majority of specimens showing differences in other respects, the two carotid arteries branch well up on the innominate. In several cases the point of origin of the left common carotid artery is close to the curve of the aorta, and in three cases (figs. 6, 8, and 10) the junction is really on the arch, thus giving rise to an additional vessel in these cases, as indicated above, which simulates very closely that found normally in the human. Three individuals (figs. 7, 9, and 10) show the formation of a thyreoid ima, so-called, a small vessel arising on the innominate between the right and left common carotid arteries, which passes forward to the thyreoid gland and gives off small vessels to the neck muscles of the region and to the trachea. Its point of origin varies somewhat in the three animals, but morphologically it bears the same position as has been described for a similar vessel in the human (McMurrich,³ p. 511.), i.e., it passes forward from the innominate between the common carotid arteries of either side. It should be said, however, that since the common carotids of either side in man differ slightly in their points of origin from those in the rabbit, the formation of this vessel in the rabbit does not contribute to the formation of a fourth vessel arising from the arch of the aorta, as is the case in man, but does form a fourth vessel from the innominate. In a single case, as shown in figure 11, the arch of the aorta gives rise to but one vessel, an innominate, which passes cephalad for some distance before it breaks to form, first, the left subclavian, and a little further forward the left common carotid artery, and the brachiocephalic artery. This peculiar variation is interesting, since it closely simulates the normal condition found in the horse. It may be explained by the fusion of the two aortic stems and the shortening of the fourth arch so that the left subclavian artery joins with the common stem during the transformation of the primary vessels. In one instance the left vertebral (fig. 3, V) takes its origin well

down on the left subclavian vessel so that it is almost in a position to be considered a separate branch from the arch of the aorta and could be interpreted as an additional vessel from the latter as has been recorded as a variation in the human (McMurrich, p. 511). It is easy to see how by a slight displacement caudad of the left common carotid artery in this case would produce four distinct vessels originating from the arch of the aorta instead of the usual two.

SUMMARY

Although the usual number of blood-vessels arising from the arch of the aorta in the rabbit is two—a so-called innominate or brachiocephalic artery and a left subclavian artery—the variations from this condition herein described indicate the possibility of a considerable departure. In one individual (fig. 11) a single vessel leaves the aortic arch, and after passing a short distance forward subdivides successively to form the left subclavian, the left common carotid, and the innominate or brachiocephalic arteries, the latter subdividing again to form the right common carotid and the right subclavian arteries.

In a number of cases, as shown in figures 6, 8 and 10, three vessels have their origin on the arch, and in these the order is the brachiocephalic, the left common carotid, and the left subclavian arteries. In one individual (fig. 3) the left vertebral replaces the left common carotid artery in the series, the carotid in this case having its origin on the innominate as normally. This case suggests the possibility of four vessels forming the series.

Conspicuous differences in the order and sequence of the vessels from the subclavian arteries of the two sides are noted. On the left side the vessels in a number of cases show a tendency to group themselves either proximally or distally in the form of a short corona, as indicated in figures 6, 9 and 10. The formation of various innominate stalks common to certain arteries are found in some cases, while in others the intervals between certain arteries are rather noticeable. Less marked variations are noted in the vessels of the right side. The vertebral artery in

one instance (fig. 2) is displaced from its usual place to the lateral side of the right common carotid artery. The transverse scapular artery in two cases is a branch of the vertebral, while the superficial cervical, which is normally a branch of the transverse scapular, in one case (fig. 10) leaves the subclavian as a common stalk with the intercostal and mammary arteries.

In three cases a small so-called thyroid ima is present, and in these this passes forward from its origin between the two common carotids, thus having the same morphological position in the rabbits as a similarly described vessel occupies in the human.

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- 2 PARKER AND HASWELL 1910 Text-book of zoology, 2nd edition, vol. 2, pp. 464-465. MacMillan Co.
- 3 McMURRICH, J. P. 1906 Morris's human anatomy, 4th edition, pp. 510-511; 556. P. Blakiston's Sons & Co., Phila.

PLATE 1

EXPLANATION OF FIGURES

1 Diagrammatic ventral view of the arteries of the thoracic region of the rabbit, showing the various branches as they occur in the majority of specimens. The innominate (brachiocephalic) (*N*) and the left subclavian (*S*) are the two usual branches of the arch of the aorta. The left subclavian gives origin to a number of arteries as here shown, while the innominate bifurcates to form the two common carotids and the right subclavian arteries.

2 Schematic ventral view of the arteries of rabbit 32, which conspicuously indicates the vertebral artery of the right side as a branch of the right carotid artery. Notice on the left side the transverse scapular and the vertebral arteries are morphologically interposed and the intercostal and mammary arteries are separated by quite an interval. The left common carotid is well down at the base of the innominate, almost constituting a separate branch of the arch of the aorta.

3 Ventral view of the arteries in rabbit 40. The vertebral artery of the left side is here formed close to the junction of the subclavian with the aortic arch, and thus forms what may be considered a third branch of the arch. The intercostal and mammary arteries of the left side are separated by a wide interval.

4 Rabbit 53 shows the formation of common stalks (innominates) for the intercostal and mammary arteries of both sides as well as the transverse and superficial cervical of the right. The brachiocephalic gives rise immediately to the left common carotid.

5 The arteries of rabbit 22 show differences in branches of the right and left subclavian vessels especially. The intercostal and mammary arteries originate separately on the right, the vertebral on the left is well cephalad of the other vessels, and makes a bend caudomesad as here shown. Accessory vessels are found on the left side also.

6 In rabbit 28 the formation of what may be termed a long corona of the left subclavian with a migration of the intercostal from the lateral surface of the subclavian to form a common stalk with the vertebral artery. The left common carotid artery is here a branch of the aortic arch so that three distinct branches are formed. The innominate is conspicuously long.

7 Specimen 19 shows among other variations the formation of the thyroid ima, a small vessel originating on the innominate just caudad to the point of origin of the left common carotid artery and passing forward to the thyroid gland of the neck.

8 Rabbit 21 shows interesting relationships of the innominate, left common carotid, and left subclavian arteries, and shows the comparatively immediate subdivision of the subclavian of either side. Such a condition may be designated as the short corona type.

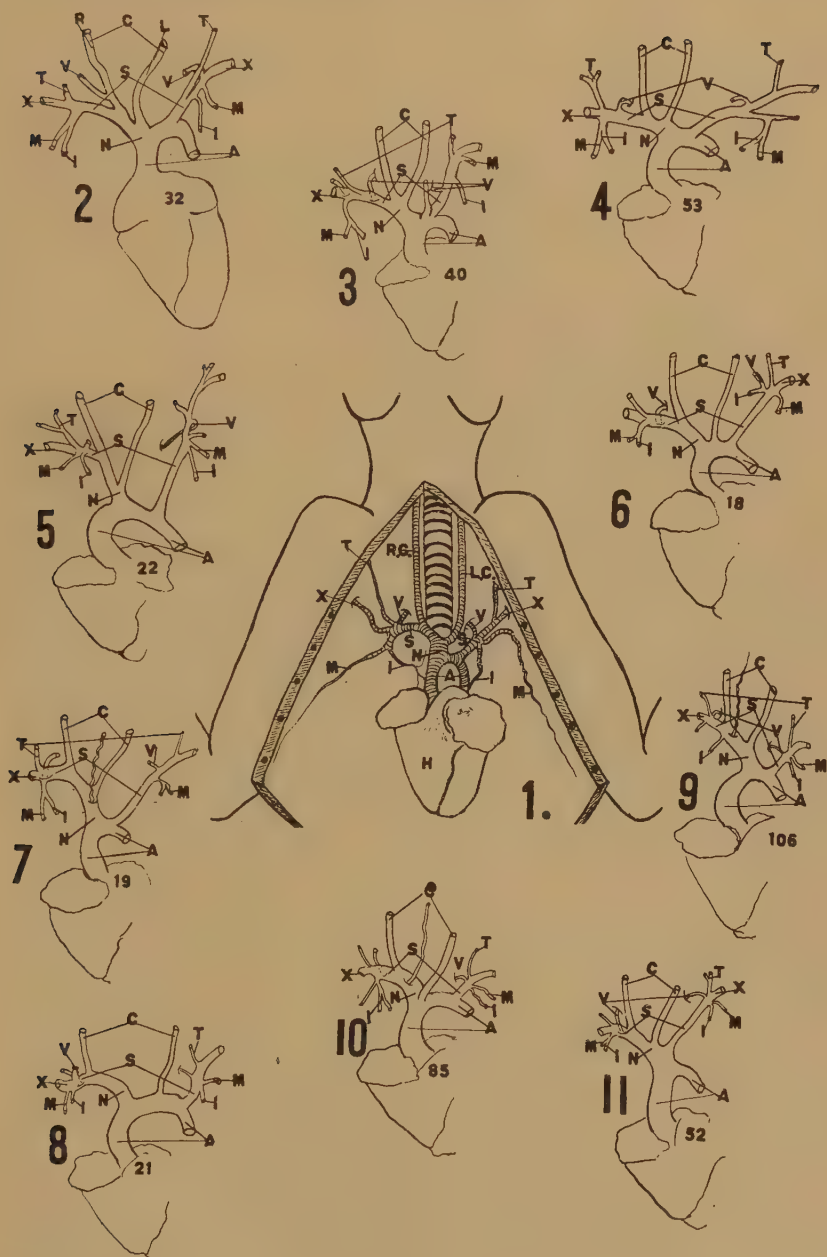
9 Specimen 106 shows the so-called thyroid ima and other minor variations especially in the interval between the intercostal and mammary arteries of the right side, and the formation of the short corona type of the left subclavian artery.

10 In rabbit 85, beside the thyreoid ima being present, the left subclavian takes its origin on the arch and the superficial cervical of the right side passes out from the common stalk of the intercostomammary artery. The subclavian of the left side forms a short corona.

11 In rabbit 52 the innominate (brachiocephalic) artery is the only vessel originating on the arch of the aorta, and subsequently subdivides as shown, giving rise to a long corona typed left subclavian, left and right carotid arteries, and right subclavian artery. This condition thus typifies that found normally in the horse.

ABBREVIATIONS

<i>A.</i> , aorta, with its ascending, transverse arch and descending (dorsal) portions	<i>M.</i> , internal mammary artery
<i>C.</i> , common carotid arteries, (<i>R</i>) right and (<i>L</i>) left	<i>S.</i> , subclavian artery, right and left
<i>I.</i> , superior intercostal artery	<i>T.</i> , transverse scapular artery, including the superficial cervical artery
<i>H.</i> , heart	<i>V.</i> , vertebral artery, right and left
<i>N.</i> , innominate artery	<i>X.</i> , axillary artery, right and left



Abstracted by Joseph M. Thuringer, author.
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A suggestion for improvement in projection and drawing
apparatus.

By substituting a focusing stage in the drawing apparatus, provided with coarse and fine adjustments, in place of the fixed stage used at present, variations in the magnification of the projected image due to focusing are eliminated, hence more accurate results in reconstruction work may be expected, even when slides and cover-glasses in a given series are not of uniform thickness. The customary arc lamp is discarded for a new commercial form of incandescent illuminant which greatly facilitates the control of the light.

A SUGGESTION FOR IMPROVEMENT IN PROJECTION AND DRAWING APPARATUSES

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ONE FIGURE

Among the various types of apparatus manufactured for the projection of microscopic objects for tracings and drawings, the Edinger drawing and projection apparatus no doubt holds first place, both from a point of usefulness and of mechanical stability. For the drawing of individual microscopic objects it leaves little to be desired, except perhaps an improved form of illuminant. However, when used for the drawing of serial sections for reconstruction work by any of the various methods in vogue, we are at once confronted with a little more difficult problem.

It is highly desirable to hold the percentage of error in reconstruction work to a minimum. A well-prepared series of sections, of course, is the essential factor. Secondly, this series should be mounted with slides and cover-glasses of uniform thickness. Even the mounting medium should be of uniform consistency and temperature for a given series, and all the slides after mounting subjected to a drying for a given number of hours at uniform temperature to insure an absolutely equal distribution of the mounting medium over the entire surface. With all these precautions carefully observed, there still remains an appreciable source of error due to the difference of magnification obtained when using the present focusing devices. The slightest change in position of the draw-tube alters the magnification. To increase the efficiency of the above-mentioned apparatus the following changes are suggested and illustrated in the accompanying drawing.

The stage as manufactured at present is only equipped with a clamp (*K*) for altering its position. This, however, does not

permit sufficiently convenient and accurate adjustment to answer the purpose of a focusing stage. The most painstaking care in the determination of the magnification by means of stage micrometer and rule will be upset by the slightest change in position of the draw-tube or by having to refocus. To obviate this source of error the focusing stage illustrated (*S*) is suggested. It is equipped with a coarse and fine adjustment identical with the one supporting the draw-tube of the microscope (*M*) and therefore not entailing great additional cost in the manufacture. This stage could also be supplied to all Edinger apparatuses in present use, thereby bringing them to their highest efficiency. After the desired magnification is once determined, all future adjustments are made by means of the stage coarse and fine adjustments. All errors due to differences in thickness of slides, cover-glasses, and mounting media are thus compensated.

The condenser (*C''*) is hinged on a support and guided by an upright which, however, is not secured to the stage, as at present, thus permitting more room for the use of a mechanical stage.

The arc lamp, which always required more or less attention and needed new carbons at the most inopportune moment, is here replaced with the new low-voltage, high-amperage, concentrated-filament, incandescent lamp. On direct current this is operated in series with a suitable resistance and on alternating current with a small transformer. Both of these devices can be attached under the drawing table and require no further attention when once adjusted.

The lamp is held by a universal support (*U*), which allows adjustment vertically as well as horizontally, thus permitting the use of various-sized lamps.

A light-tight, ventilated hood, provided with an adjustable reflector (*R*), completes the outfit.

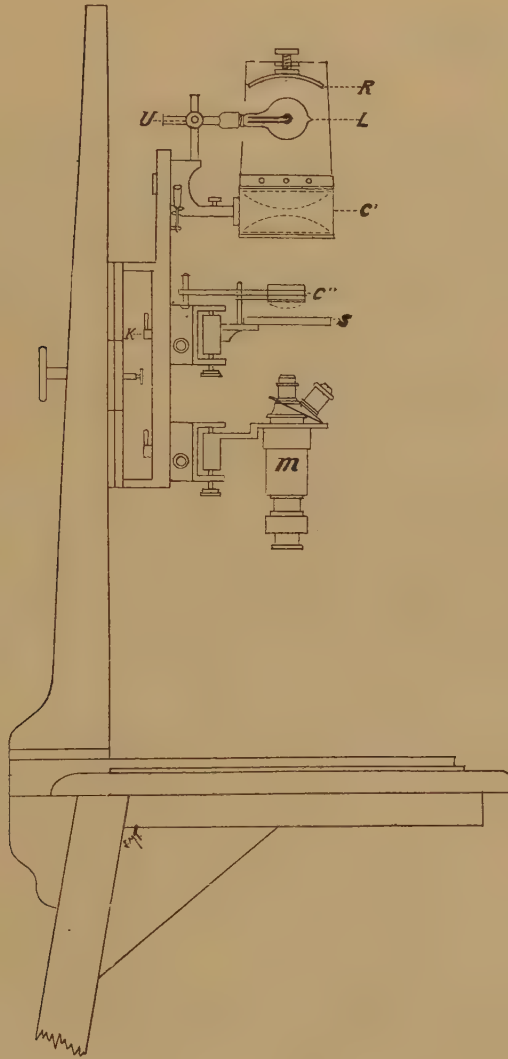


Fig. 1. Diagram of projection and drawing apparatus. *C''*, stage condenser; *C'*, condenser; *L*, lamp in ventilated housing; *R*, adjustable reflector; *U*, universal support; *S*, focusing stage; *K*, clamp; *M*, microscope.

Abstracted by James C. Watt, author.
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Symmetrical bilateral dystopia of the kidneys in a human subject, with outward rotation of the hilus, multiple arteries and veins, and a persistent posterior cardinal vein.

In a male human subject, aged twenty-eight, who died of pulmonary tuberculosis, an associated series of rare anomalies of the kidneys was found. There was a symmetrical bilateral displacement caudally, each kidney lying from the level of the second to the fifth lumbar vertebrae. Symmetrical displacement without fusion is rare. The hilus forms a long, narrow groove, the upper part lying on the anterior surface of the kidney, the remainder describing a spiral cutting around the outer border on to the posterior surface as it proceeds caudad. This lateral position of the hilus is extremely rare, previous ones being found in pelvic kidneys, and very few instances being recorded. On the right side were five renal arteries, two off the aorta, three from the common iliac artery. There were four left renal arteries, two from the aorta, one from the common iliac, and one from the hypogastric arteries. Two spermatic arteries were present on the right side and three on the left. Two renal veins, uniting into a short common stem tributary to the inferior vena cava, occur near the upper pole of each kidney. In addition, on the left is a posterior cardinal vein connected at the ends to the common iliac and upper renal veins and having as tributaries a third renal vein and four lumbar veins. A fourth left renal vein goes to the hypogastric vein. The pelvis of the ureter enters the kidneys anterior to the main vessels. The ureter courses lateral to the kidney.

SYMMETRICAL BILATERAL DYSTOPIA OF THE KIDNEYS, IN A HUMAN SUBJECT, WITH OUTWARD ROTATION OF THE HILUS, MULTIPLE ARTERIES AND VEINS, AND A PERSISTENT POSTERIOR CAR- DINAL VEIN

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TWO FIGURES

In the laboratory of the Department of Anatomy of the University of Toronto a very interesting series of associated anomalies relating to the kidneys and their vessels was discovered during the regular course of dissection. The specimen was at once put aside for investigation, and on further study has been considered worthy of a detailed description.

The body was that of a well-proportioned but somewhat emaciated male, aged twenty-seven, who died of pulmonary tuberculosis. Apart from the abnormalities associated with the kidneys, no other gross anomalies were noticed in this subject.

THE KIDNEYS

Shape and size (fig. 2)

The outline of the kidneys is that of a long, narrow oval. The ventral surface is quite convex, the dorsal surface flattened. Of the two poles, the lower is much thicker than the upper. A shallow groove winding spirally from the ventral surface laterally and caudally on to the dorsal surface forms the hilus, and notches the outer border where it crosses it. Except for the presence of the hilus, the surface is smooth, and shows no special lobulation.

The measurements taken are as follows:

	Right kidney	Left kidney
Greatest length.....	10.5 cm.	11 cm.
Width.....	3.5-4.5 cm.	3.5-4.5 cm.
Thickness.....	2.5-3.5 cm.	2.5-3.0 cm.

Position and relations (fig. 2)

The two kidneys exhibit a displacement which is quite symmetrical on both sides. Each lies close in against the psoas

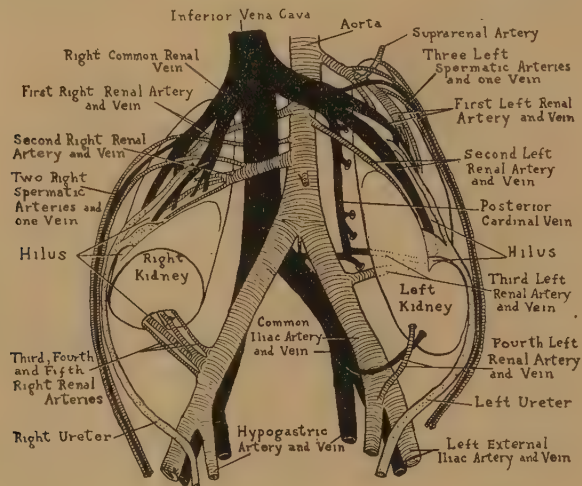


Fig. 1 Outline drawing of the kidneys and their vessels and ureters. Veins are solid black, arteries striped, and ureters stippled. Lower part of right kidney removed.

major muscle and shows the same degree of obliquity as the muscle. The upper pole of each kidney is about 1 cm. nearer the midline than the lower pole. The upper pole is opposite the middle of the second lumbar vertebra, the lower opposite the lower part of the fifth lumbar. The kidney thus lies with its upper portion in the lumbar region, on the quadratus lumborum muscle, the other portion in the iliac fossa, on the iliacus muscle.

The suprarenal glands were placed over the upper pole and slightly to the medial side of each kidney. The left gland was

situated in a small space with the kidney below, pancreas above, spleen laterally and vertebrae medially.

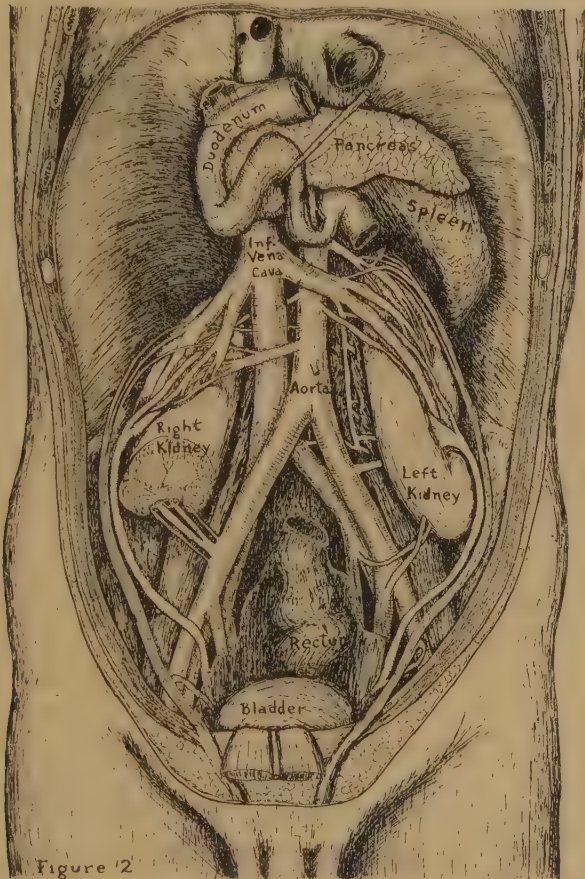


Fig. 2 Drawing of the kidneys to show their relations to the dorsal abdominal wall and the viscera. The duodenum, pancreas, and spleen have been retained in position, the lower part of the duodenum being hooked up to expose the underlying vessels. The suprarenal glands have been removed to expose the upper pole of the kidney. Lower part of right kidney removed.

The pancreas was situated entirely above the left kidney and crossed right over the spleen. Owing to the downward displacement of the kidney, the spleen was displaced inward and

was in contact with the vertebrae medially for two-thirds of its length. The lower pole, however, had the upper pole of the kidney inserted between it and the vertebral column.

On the right side the kidney and suprarenal gland lay entirely below the level of the liver, which was thus allowed to come into contact with the diaphragm on its posterior surface.

The upper pole of each kidney and the common renal vein from each side were under cover of the duodenum at the flexure of the latter at the lower end of the descending limb.

The hilus (fig. 2)

The position of the hilus is most interesting, and is quite similar on both sides. Starting above, about three centimeters below the upper pole, on the anterior surface, it runs obliquely caudad to cut the lateral border of the kidney, forming a notch on it about two thirds of the way down. It then curves from here on to the posterior surface, ending about two or three centimeters from the lower end of the kidney.

The hilus is thus placed on the opposite border to the normal and forms a spiral with gradually increasing rotation about the polar axis as it proceeds caudad.

• VESSELS

Arteries (figs. 1 and 2)

The renal arteries and also the spermatic arteries of both right left sides are multiple.

Right side. The right renal arteries are five in number. The first comes off the abdominal aorta at the level of the second lumbar vertebra and goes behind the inferior vena cava to the upper end of the hilus on the anterior surface of the kidney. The second renal artery also goes to this surface, coming from the aorta at the level of the third lumbar vertebra and running in front of the vena cava.

Off the right common iliac artery come the third renal artery, a very small one, the fourth, quite large and dividing early into

two, and the fifth, a small artery again. These three arteries running in close company pass behind the lower pole of the kidney and enter the lowermost part of the hilus on the posterior surface.

The right spermatic arteries are two in number. The higher one arises from the aorta between the first and second renals, and runs posterior to the inferior vena cava and both renal veins, but anterior to the upper pole of the kidney. The lower artery arises from the second renal, goes posterior to the inner renal vein, anterior to the outer vein, and anterior to the kidney. At the lateral border of the kidney the two spermatic arteries and the vein form a common bundle running in contact with this border and the ureter in the iliac fossa, and then turning over the psoas muscle to the internal abdominal ring.

Left side. There are four left renal arteries. The first is off the aorta at the upper limit of the second lumbar vertebra and runs down anterior to the upper pole of the kidney. The second artery is from the aorta, over the second lumbar vertebra, level with the highest artery on the right. It is also to the hilus on the upper part of the anterior surface of the kidney.

The third left renal artery is off the left common iliac, and is peculiar in that it runs across the upper part of the iliac fossa behind the kidney, to pass into the hilus just where it cuts across the lateral border.

The fourth artery is off the internal iliac, or hypogastric artery, just at its commencement, and runs anterior to the external iliac artery and psoas major muscle and penetrates the kidney on its medial border just near the lower pole.

On this side there are three spermatic arteries, the highest coming off a suprarenal branch of the first renal, the other two directly off the first renal. All three arteries and the spermatic vein form a common bundle coursing anteriorly along the lateral border of the kidney, then lateral to the ureter in the iliac fossa and down to the inguinal canal.

Veins (figs. 1 and 2)

Right side. There are two renal veins, both coming from the upper part of the hilus over the anterior surface of the kidney, and uniting at the level of the upper pole of the organ into a common vein which is about three-quarters of an inch in length and empties directly into the inferior vena cava.

The right spermatic vein, a single vessel, opened into the lateral of the two renal veins.

Left side. On this side are three renal veins. Two are quite similar to those on the right, arising from the anterior surface of the kidney on the upper part of the hilus and uniting into a common stem which crosses anterior to the aorta and empties into the inferior vena cava.

Just at the junction of the above two veins, there comes into the medial one, a longitudinal vein which lies over the front edge of the psoas muscle, on the vertebral column, in the interval between the aorta and the left kidney. This stem starts at the level of the fifth lumbar vertebra, and communicates with the left common iliac vein below. As it ascends it receives as tributaries four lumbar veins, one of which is double, and also a renal vein. This renal vein comes from the hilus where the latter cuts the outer border of the kidney, and runs medially posterior to the kidney, alongside of the third renal artery, and ends in this ascending vein. This longitudinal stem is interpreted as a persisting portion of the embryonic posterior cardinal vein of the left side, which lies exactly in the position occupied by this present vein.

The left spermatic vein, single in spite of the presence of three arteries, empties at the junction point of the two large upper renal veins into the common trunk.

Ureter (figs. 1 and 2)

The position and relations of the ureter are remarkably symmetrical on the two sides.

At its pelvis, each ureter is divided into two parts. One is a long, narrow, tubular portion which lies in the upper part of

the hilus, on the anterior surface of the kidney. The other is a broad, short, funnel-shaped portion communicating with the kidney in the hilus just before the latter cuts round the outer border of the organ.

The two parts unite at the lateral border of the kidney, which the ureter now follows to the lower pole, where it then crosses the iliac fossa, turns medially over the psoas muscle and external iliac artery into the pelvis, where its course into the bladder is normal.

The highest artery and the lateral vein accompany the upper branch of the ureter as it enters the kidney, the vessels lying behind. The other vessels enter the kidney mostly behind the lower branch of the ureter.

SIMILAR CASES

Multiple renal arteries and veins in all the locations found in this case have been previously described and discussed by various authors, and so call for no special consideration. Tonkoff ('03), for instance, describes and gives a figure of a right kidney slightly displaced downward and with an arrangement of its four renal arteries almost identical with those of the left kidney in this case.

Macalister ('83) and Morris ('85) both state that abnormal vessels occur in three individuals out of every seven.

The occurrence of a vena cardinalis posterior along with renal anomalies has been noted before. Melissinos ('11) found a case of pelvic kidney with a persistent right cardinal vein, and gives reference to a few other instances.

The presence of the rotation seen in these kidneys, on the contrary, is evidently quite a rare condition. Among the anomalies of position of the hilus, the particular one exhibited here is not even mentioned in the text-books on pathology or surgery. It is self-evident that such a position would be of great interest, especially to the surgeon.

Gerard ('05), in a review of 527 cases, states that the renal hilus, instead of lying medially, may be superior, inferior, ventral, or dorsal, but does not mention any instance of a lateral position.

Müllerheim ('02) describes a case where the left kidney was found in the pelvis, with its hilus not medial, but anterior, and he states that one of the characteristics of dystopia of the kidney is that the hilus is usually anterior in position.

Morris ('04), in a summary of displacements, states that the kidney may be rotated so that the hilus looks upward, outward, directly forward or backward, and mentions one case of the hilus occurring laterally. This case was described by Farquharson ('94) as a left kidney placed in the pelvis with hilus looking to the left.

Brown ('94) also describes a right pelvic kidney which had rotated till its posterior surface had become anterior and the hilus looked posteriorly to the right. Johnson ('14) described a case in the cat exactly similar to that of Brown's and Anitschkow ('12) describes and gives a figure of a left kidney in man displaced slightly back in the lumbar region and with a hilus which he describes as anterior, but which, in the illustration, appears to course around the lateral border, as there is a marked indentation shown there.

McMurrich ('98), considering a series of crossed dystopia of the kidneys with fusion, pointed out that in nearly all cases the position of the hilus was anterior.

This retention of an anterior position of the hilus in displacements and in fusions of the kidneys is the retention of the normal embryological position. Pohlman ('05) noted that until the kidney had ascended in the embryo to where it was approximately in the adult position, the hilus was ventral, and then a rotation medially of 90° occurred about the polar axis. Felix ('12) also states that this rotation occurs, but that a reverse rotation toward the ventral surface also occurs later, so that the hilus is finally ventromedial.

The kidneys in the present case have not reached the usual final level and so might be expected to have retained the hilus anteriorly. This is true of the upper part, but the lower portion exhibits the rare outward rotation through 90° to bring it laterally, and the lowest part goes even further than this to lie posteriorly. There is thus considerable torsion in the kidney, the hilus forming quite a spiral in its course.

The fact that the ureter lies ventral to the main renal vessels at the hilus at first sight appears as an anomaly. It will be seen, however, that if the hilus were to be rotated into its usual position the ureter would then lie posterior to the vessels. Thus at their entrance into the kidney these structures stand in their normal relations to each other, but the rotation makes them appear reversed.

The position of the suprarenal glands is interesting. McMurich, Morris, Müllerheim, and others have all stated that the relation of these glands to the kidneys is merely topographical and that they are found in their usual places in cases where the kidneys are displaced. In this instance, however, they lie closely capping the upper pole of each kidney, and so are displaced somewhat caudally from their normal location.

What was the actual cause of all the anomalies shown above is open to conjecture. It must have been a force acting in early embryonic life. The displacement into the iliac fossa was probably due to lack of growth in the ureter and the torsion due to a twisting of the pelvis of the ureter. It is of interest to note that Felix ('12) states that in the lumbar region the ureter shows a dilatation accompanied by a spiral twisting. An exaggeration of this process might possibly account for the result shown here. Whatever the cause may have been, the result is most remarkable for instead of a symmetrical displacement of the whole organ, we have here the upper pole with the upper end of the hilus facing still in the old embryological position, while proceeding caudad there is an ever-increasing torsion evident, until finally at the lower end the hilus shows a displacement of 180° brought about by lateral rotation.

The position of the kidneys in the lower lumbar region and iliac fossa seems to be a much rarer condition than the position within the pelvis, as by far the greatest majority of cases of dystopia without fusion are reported as being in the pelvis.

The symmetrical degree of dystopia shown by these two kidneys seems to be almost as rare a condition as the lateral hilus. In all the cases quoted above and in many others not mentioned here, if the two kidneys are not fused to form the discoidal or the

horseshoe kidney, either there is a much greater degree of dystopia on one side than on the other or else only one kidney shows displacement, the other being in its normal position. Thus the kidneys in this instance are unique in several respects and have therefore seemed well worthy of description.

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Resumen por el autor, Eben James Carey.
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Estudios sobre la dinámica de la histogénesis. La fuerza que motiva el crecimiento como estímulo dinámico en la génesis de los tejidos esquelético y muscular.

La región activa dominante en el crecimiento del intestino es el tubo epitelial; la zona que crece menos activamente es el mesenquima que le rodea. En el colon terminal del cerdo el tubo epitelial crece en dirección caudo-cefálica. Las figuras mitóticas siguen en su mayor parte la dirección de una hélice sinistrorsa. En embriones de cerdo de 10 a 25 mm. de longitud, el colon terminal crece relativamente con mas rapidez en diámetro que en longitud. Durante este periodo la túnica interna de músculo liso está en periodo de formación. Cuando el embrión crece desde los 25 a los 45 mm. el colon terminal crece mas rápidamente en longitud que en anchura. Durante este periodo de alargamiento intestinal rápido se inicia la capa externa de músculo liso. La correlación del crecimiento tubular epitelial en longitud y anchura, con la génesis de las túnicas musculares lisas interna y externa, respectivamente, se considera bajo el aspecto de "fuerza que motiva el crecimiento." La región de crecimiento acelerado en el miembro en vías de desarrollo es el núcleo esquelético central; la de crecimiento retardado es el mesenquima que le rodea, el cual se transforma ulteriormente en la musculatura y tejidos conectivos relacionados con ella. Estas dos zonas de crecimiento diferencial se influyen mutuamente, y esto es evidente objetivamente a causa de un cambio de movimiento y por una alteración de la forma externa y estructura interna de las células afectadas. El primer material óseo del embrión se distribuye económicamente en la periferia al principio, sobre la superficie convexa mas débil del fémur curvo. Después el hueso envuelve al centro de la diáfisis y aparece en el lado cóncavo del fémur cartilaginoso curvo. La correlación entre el crecimiento esquelético acelerado y el desarrollo mesenquimático retardado se considera con referencia a la "fuerza que motiva el crecimiento diferencial."

STUDIES IN THE DYNAMICS OF HISTOGENESIS

GROWTH MOTIVE FORCE AS A DYNAMIC STIMULUS TO THE GENESIS OF MUSCULAR AND SKELETAL TISSUES

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TWENTY FIGURES

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INTRODUCTION

The principle of unequal growth constantly confronts the embryologist in his investigations. The local thickenings and foldings of the central nervous system, the unequal growth of the cardiac septa, the elongated intestinal tract, are common instances exemplifying the principle that the body parts develop at different rates.

This idea was recognized by Aristotle, but was not definitely formulated until 1774 from Wolff's convincing studies. In the latter's work on intestinal development the principle of unequal growth was definitely established and elaborated considerably. In 1874, His compared the various layers of the chick embryo to plates and tubes of an elastic nature. From these he suggested that some of the principal organs are molded by local zones of unequal growth. Davenport ('96) resolves the changes in ques-

tion into movements of cells or cell aggregates, the latter being linear, superficial, or massive. He still further classifies each of these three divisions.

These local zones of unequal growth and the movements of cells have been looked upon by Herbst ('94) and Dreisch ('94) as physiological responses to definite stimuli. His and Davenport as well as Roux ('95) aim at something more than a mere description of unequal growth and ontogenetic events. They made an attempt to give a mechanical causal explanation for these processes. The function and aetiology were considered side by side with structure.

It is from the dynamic view-point that the present investigation was pursued. It is desired to emphasize the fact that in zones of unequal or differential growth, in limb and intestinal development, that an interaction of forces takes place, resulting in a transference of energy, and that these forces are factors in histogenesis. This action and reaction and transference of energy is due to a definite entity, growth motive force, a term introduced by the writer.

Growth motive force is any agency which tends to produce a transfer of kinetic energy, from an active to a less active group of cells, and of potential energy from a less active to an active group, in a cellular field of differential growth until equilibrium is established. The active and less active zones are in reference to the rate of cell division per millimeter of cross-section. This principle was deduced from a series of studies on osteogenesis and myogenesis begun in 1914. Previous reports of a part of this work have been presented to the Association of American Anatomists (Carey, '17, '18, '19).

The understanding of the causes underlying tissue formation or differentiation of an unspecialized cell is the central difficulty for the student of development.

The increase of cellular components, the transformation of these, and the perfection of form out of the relatively formless antecedents are phenomena which demand the closest analysis. Growth and division of the nucleus, however, are merely changes concomitant with the specialization which the cell undergoes.

There are three theories regarding cellular differentiation: first, the 'mosaic theory' of Roux ('88), later modified by Wilson ('04), Conklin ('05), Zeleny ('04), and Boveri ('04); second, the 'organization theory' of Whitman ('93) and more recently elaborated by Child ('15) in the latter's studies on metabolic gradients and individuality; third, the 'homogeneity theory' of Dreisch ('91-'93). Dreisch considers the peculiar organizing quality of protoplasm as due to the expression of a mysterious force wholly different from any in the inorganic world.

At least in certain of the earliest stages, the primordial cell is modified during development by the environment. It is not independent in its development but is dependent upon an interaction of developing parts before its external form and internal structure are perfected. This is the theory expressed by the terms, mutual interaction, correlation, interdependents, dependent differentiation or differentiation due to position. This theory is upheld by His ('74), Hertwig ('94), Fischel ('98), Von Baer (1828), Pfluger ('83), C. Schultze (1900), Hans Dreisch ('94), Zoja ('95), Whitman ('94), Child ('99) and Thoma ('07) and to a limited extent by Roux. The latter investigator distinguished two periods in the development of the body parts: first, a period of self-differentiation in which the parts arise, grow, and differentiate of themselves; second, a period of functional form development in which the more complete formation of the parts is accomplished through the influence of stimuli.

As to the first view, it has been convincingly proved that there are organ-forming stuffs in the cytoplasm. Wilson ('04) concluded from his studies that the cytoplasm of the primordial germ cell contains certain specific organ-forming stuffs which have a definite arrangement. These observations of Wilson have been confirmed by Conklin ('05), Zeleny ('04), Boveri ('04).

The third theory regards differentiation as dependent upon either an extrinsic or an intrinsic factor. Differentiation so considered is in the nature of a physiological response to a stimulus. The structure of the reacting as well as of the stimulating body, however, contributes to the quality of the effect. Specialization by this method is simply an 'induction,' according to Dreisch.

It is an effect produced upon the parts that are developing by other developing parts or by an extrinsic factor in the environment. Three elements are consequently involved: first, the stimulus; second, the reception of the stimulus; third, the response. The first is some other organ or external agent; the second and third are functions of the organ in process of formation. Lack of evidence has been the chief obstacles to the acceptance of Dreish's theory of induction.

The term 'induction' implies an effect or change produced without contact. But, in respect to the primordium of the muscular and skeletal tissues, there is a definite syncytial continuity. Consequently, any effect produced by either tissue upon the other would be through 'conduction' and not through 'induction.'

In this action, through conduction of the developing skeletal and muscular tissues upon each other, the factor of force is inherently involved. The primordial blastemal skeleton is undergoing the most rapid growth, as a consequence of which a tensional elongating or stretching action is bound to be exerted upon the surrounding and less actively growing, continuous, syncytial mesenchyme. It is desired, therefore, to emphasize the following facts:

First, that there is a force manifested by rapid skeletal growth.

Second, that this force exerts a tensional or stretching action upon the surrounding mesenchyme, influencing the first steps of myogenesis.

Third, that the first differentiated muscles react upon the primordial blastemal skeleton resulting in a definite series of changes. These are seen in the formation of the condensed cartilaginous skeleton and later, as the muscles become more developed and vigorous in physiological function, in the formation of the osseous skeleton.

This action and reaction of forming parts results in the condition that at any period of development the degree of differentiation of the musculature and skeleton represents an equilibrium established between opposing myogenic and skeletal forces. Mechanically, therefore, skeletal and the related muscular tis-

sues are interdependent, one relying upon the other for its initial and continued differentiation.

The foregoing applies to the skeleton and skeletal cross-striated musculature. Concerning the smooth muscle of the intestine there is a similar interaction of differential forming parts. The epithelial lining of the alimentary tube is the most active region of growth. The growth in diameter in the early stages is due almost entirely to the rapid degree of mitosis of the epithelium and not to the surrounding mesenchyma forming the bulk of the wall. As a consequence the lumen rapidly increases in diameter, and it is this increase which causes primarily the diametrical growth of the intestine. It is readily apparent that the rapid distention of the lumen due to epithelial growth would cause a tension upon the relatively passive, contiguous, syncytial mesenchyme. This action would tend to draw out or stretch the mesenchymal cells in a concentric manner somewhat similar to the tension put upon the strained elastic fibers of a rubber balloon when distended with air, the pressure of epithelial growth being comparable to the air pressure.

Once the encircling mesenchymal cells have formed a definite ring, the expanding lumen would meet a resistance to growth in diameter. The growth force, pursuing the lines of least resistance, would be directed in a longitudinal manner due to the shifting of the planes of mitosis from a longitudinal to a transverse direction. This shift is directly due to the external resistance of the first-formed ring of inner circular smooth muscle.

At this point the term force is one that will stand close scrutiny and careful thought on the part of the embryologist. A force is one of a pair of equal, opposite, and simultaneous actions between two bodies by which the state of their motions is altered or a change in form in the bodies themselves is effected. Pressure, attraction, repulsion, and traction are instances in point. Muscular sensation conveys an idea of force, while a spring balance gives an absolute measure of it, and a beam balance only a relative measure. In accordance with Newton's third law of motion that action and reaction are equal, opposite, and simultaneous, forces always occur in pairs.

Force is exerted in certain regions of the embryo by the genesis of a rapidly dividing group of cells upon a less active or relatively passive group of cells. In turn the relatively passive group react upon the former. This action and reaction is objectively evident by a retardation or alteration of the rate of growth or by a change produced in the external form or internal structure of the cells involved.

The most rapidly dividing group of cells in a differential growing cellular field in syncytial continuity is subjected to a force tending to direct it in the path in which the resistance diminishes most rapidly, that is in the direction of a line of force. The most rapidly growing cells raise the kinetic energy of the field at the point of rapid growth above that of surrounding points, and hence a transference of energy takes place until equilibrium is established. There will be a transfer of kinetic energy from the growing to the passive group of cells resulting in an elongation of the latter and a consequent storage of potential energy due to position. On the other hand, there will be a transference of potential energy from the elongated relatively passive group of cells to the moving or growing group which will tend to restrict or retard the motion or growth of the former. This motive force of genesis, growth, and differentiation continues until the difference in energy disappears.

These biological generalizations are analogous to electromotive force. If two metal spheres at different potentials be connected by a wire, a transfer of positive electrification will take place from the one of higher to the one of the lower potential, or a transfer of negative electrification from the one of lower to the one of higher potential, or of both, until the difference of potential disappears. The higher and lower electrical potentials are analogous to the continuous zones of rapidly dividing and less active group of cells, respectively. The term electromotive force is applied to any agency which tends to produce a transfer of electrification as exemplified above. Growth motive force consequently may be defined as any agency which tends to produce a transfer of kinetic and potential energy in a cellular field of differential growth.

EARLY STAGES IN THE HISTOGENESIS AND MORPHOGENESIS OF
THE DESCENDING COLON OF THE PIG (*SUS SCROFA*)

The increase or decrease in size of certain parts of the intestine and the cellular transformations which occur are of fundamental importance. By analysis and careful description of the changes which occur in sequence and by subsequent synthesis of the data obtained, an interesting correlation in dynamics is thereby detected. Heretofore investigators of histogenesis have had independent and isolated view-points in their work on intestinal development, no correlation of the developmental processes being attempted. The admirable descriptive observations on intestinal development by McGill ('07) and Johnson ('11) fulfill the purpose of their respective authors, but lacked interpretation and correlation of the facts observed. Their point of view was descriptive morphology, not dynamic.

In an embryo 10 mm. in length the descending colon presents in cross-section an oblong oval or pear-shaped appearance, the convexity of which is directed toward the interior of the abdominal coelomic cavity. The tapering end is attached to the dorsal abdominal wall through the intermediation of the relatively long and thick dorsal mesentery. There are three main elements which demand close attention (fig. 1). The first of these is the inner epithelial tube; the second, the outer peritoneal epithelium, and the third, the intermediate mesenchymal zone.

The inner epithelial tube in cross-section is oval in shape containing a narrow oblong lumen with rounded ends. The lining cells of this tube form from two to three rows of nuclei. Mitosis is usually found in the superficial row of cells. At this stage mitotic activity is prominent in the epithelial cells. The basal row of cells rest upon a well-marked basement membrane.

This basement membrane is directly contiguous to the intermediate mesenchymal zone. In this zone no clear-cut cell is found. The entire region is composed of protoplasm in syncytial continuity, embedded in which are found the nuclei. The nuclei are oval or round and present a very dense network of chromatin, especially well seen when stained with iron-hematoxylin. The membranes of the nuclei are decidedly distinct. The protoplasm

is granular, presenting an irregular network structure. Scattered in the mesenchymal region are seen isolated discrete vesicles. These are especially congregated toward the dorsal mesenteric attachment. The vascular vesicles are variable in size and shape and present various degrees of confluence.

The thickness of the mesenchymal wall is nearly twice that of the diameter of the epithelial tube. It is to the rapid increase in diameter of the latter, due to rapid epithelial mitosis, that the increase in width of the intestine is to be ascribed. The mesenchyme remains relatively passive, and as a consequence is put under great tension by the internal distention of the epithelial tube.

Attention is especially directed to this difference in the rate of growth between the inner epithelial lining and the intermediate zone of mesenchymal cells. The continued differentiation of the intestine is pivoted upon this fact. Furthermore, the epithelial distention is not a uniform one. Mitosis takes place in a spiral manner from the anal toward the ileocecal valve. Consequently, the rapid growth of the epithelial tube is a specific type from below upwards.

The attention of the writer was directed to the fact, after plotting hundreds of intestinal epithelial mitotic figures, that these figures were usually confined to some definite region of the circumference of a single section. This region was found to change at different levels of the serial sections. By graphic reconstruction (sections 45 to 94) this plot was found to form the path of a definite spiral describing a dextrotropic rotation in one case; in nineteen others the path was a left-handed spiral. The spiral itself presented a head or apical region in which mitotic figures were found to be numerous and a tail or basal end in which there were fewer and fewer figures. The apical end of the spiral path is always directed toward the ileocecal valve and the basal end toward the rectum. Growth is therefore from below upward in a spiral course. One spiral growth is quickly followed by a second which rifles a path slightly lateral to its predecessor. This in turn is followed by a third, in a path still more lateral, and so on around the circumference. This intermittent rhythm

of explosive spiral growth may be compared to that of the successive fire balls emitted by a roman candle in fireworks. The paths formed by this explosive spiral growth may be compared to those within the barrel of a Winchester rifle.

Lining the outer peripheral portion of the mesenchyme is the peritoneal epithelium. In the 10-mm. embryo this is a single layer of oval or cuboidal cells. These are continuous from the dorsal mesentery and envelop the primitive colon proper. The cell walls of this layer are contiguous and give a beaded appearance to the peritoneal epithelium. Later in development this cellular layer becomes flattened and markedly elongated, the individual cells becoming more and more attenuated and spindle-shaped.

The beginning of this flattening or elongation of the peritoneal epithelium is seen in a 14-mm. embryo (fig. 2). This cross-section represents the corresponding region of the descending colon in the 10-mm. embryo described above (fig. 1). In addition to the elongation of the nuclei, the cytoplasm is drawn out into a fine membrane between the separated nuclei. At the same time that the peritoneal epithelium is elongated, the epithelial tube is seen to have grown double in size, whereas the mesenchyme has only increased one-half that of the former stage observed.

The lumen of the epithelial tube is directed more transverse than vertical to the long axis of the gut. The lining cells appear to be overcrowding at the lower pole of the lumen due to rapid mitosis. This condition gives a stratified appearance to the epithelium. This rapid mitosis constantly causes an increase of free surface, and consequently the lumen rapidly dilates in width.

Concomitant with the rapid increase in width of the epithelial tube, there is observed a change in shape and rearrangement of the surrounding mesenchymal cells. The nuclei and surrounding granular protoplasm become elongated in a definite direction. Instead of the irregular arrangement characterizing the oval nuclei and stellate cytoplasm before, there is now observed a definite tendency for the cells to form concentric layers. This tendency is more marked in the midzone of the mesenchyme between the epithelial basement membrane and the outer simple epithelial peritoneum. In this midregion there is a condensation

more definite at the upper (fig. 2) than at the lower pole of the epithelial tube and greater in either polar region than on the lateral aspects of the tube.

With a further absolute increase in diameter of the epithelial tube (fig. 3) over that of the intestinal wall, the smooth muscle elements become more elongated, flattened, and spindle-shaped, and the definitive inner circular smooth muscle layer becomes more clearly defined out of its former nebulous state (fig. 2). By actual measurement with the filar micrometer, the intestinal wall is seen to become thinner as the epithelial tube constantly increases in size. The embryo is now approximately 20 mm. in length, and during this period it is convincingly seen that the long axis of the elongated nuclei are arranged along the paths of concentric circles. The longitudinal granular fibrils are likewise arranged in this concentric manner.

With the constant increase in width of the epithelial tube there is a progressively greater and greater elongation of the muscle elements—nuclei and granular fibrils. These fibrils branch and anastomose with neighboring fibrils, and constantly maintain the original continuity of the protoplasmic syncytium. With the ever-increasing tension of the fibrils there is a progressive loss of water and increase in viscosity.¹ Definite physico-chemical changes take place in the granular fibrils resulting in condensation and fusion of the granules into a continuous coarse irregular strand. Near the nuclei the swellings upon the strand are marked, but toward the poles of the nuclei the fibrils are more attenuated.

As formerly reported by McGill, there is the same tendency in the development of the colonic muscles to form coarse and fine myofibrils as detected in the oesophagus. These fibrils are of variable length and run through several neighboring cells in many cases. The coarse and fine granular fibrils are seen side by side. The coarser ones being primarily located at the periphery of the ill-defined spindle cell, whereas the finer granular myofibrils are located more internally and nearer to the nucleus. Between the fibrils more or less undifferentiated granular cytoplasm persists.

¹ The chemical changes in myogenesis will be reported later with my colleague in biochemistry, Victor E. Levine.

In embryos, between 24 and 46 mm., the descending colon increases rapidly in length. Peripherad to the inner smooth-muscle coat there is found the beginning of elongation of cells similar to that described for the inner smooth-muscle coat. Similar changes in shape and arrangement of the components take place, however, in a longitudinal rather than in a transverse plane. At first this layer is more or less uniform throughout (figs. 3 and 4), but there is soon detected a greater proliferation of cells immediately underlying the dorsal mesentery. This aggregation of cells represents the inception of the longitudinal mesenteric taenia coli band of fibrils. This is definitely seen in figure 6.

The initial genesis of the mesenteric taenia coli before the other bands appear is significant. If we remember that this location represents the outer curvature of a coiled tube in the process of rapid formation, it is readily seen that more definite tension of differential growth is exerted at this location. These bands are more definitely developed nearer the ileocecal valve. The dynamics involved will be considered later.

The longitudinal muscle, however, is only slightly developed at 28 mm., and at 45 mm. is not as conspicuous as the myenteric Auerbach's plexus. This plexus is located between the well-developed circular smooth-muscle coat and the attenuated outer longitudinal-muscle coat. The nerve plexus at these stages 10 to 46 mm. is composed of a continuous layer of groups of cells with crowded nuclei and many non-medullated fibers.

The inner submucous plexus of Meissner is not as prominent as the outer one. It is similarly constructed, although it contains fewer and much smaller ganglia and the meshes of the plexus are much finer. The terminal nerve fibers were traced to the epithelium and between the epithelial cells at 46-mm. stage. The plexus first appears along the inner border of the inner circular coat.

The muscularis mucosa is not differentiated at 45 mm. The lymphatic channels, however, are abundant at 32 mm. along the line of the mesenteric attachment. Lymphatic nodules are not formed, on the other hand, in the submucosa until the 150-mm. stage is reached.

The lumen of the descending colon is patent throughout development; no sign of atresia is observed. Between the 10- and 14-mm. stages small vacuoles were found, but no diverticulae are seen. At 10 and 14 mm. the colon is round or slightly elliptical in shape, gradually enlarging toward the cloaca. The lumen possess in the earliest stages a shape comparable to that of the entire tube. Between 53- and 46-mm. stages, however, lateral, evaginations are developed which give the lumen a crucial instead of a round or elliptical appearance. These evaginations push out at the lateral aspects where the circular muscle is least developed, along lines of least resistance. At the dorsal and ventral poles of the lumen the smooth muscle forms a thicker layer than on the lateral aspects. In addition, resistance is still further increased by the formation of the longitudinal mesenteric taenia along the dorsal, attached margin of the descending colon.

GROWTH MOTIVE FORCE IN INTESTINAL DEVELOPMENT

In the inorganic world that which produces motion or pressure is considered as due to a force. This entity has already been defined. One result of its action on an elastic body, namely, a strain, should now be considered. This is imperative, for if mechanical forces are at work on organic matter they tend to produce similar results as those acting upon inert matter. Too frequently the term self-differentiation is applied to alteration of form and internal structure of developing cells without searching the immediate environment of the specializing cells or syncytium to ascertain whether or not these changes are attributable to forces outside of the differentiating zone. This applies particularly to the differentiation of bone and muscle tissue. If a cell changes in form successively through the spherical, ellipsoid, and spindle stages it undergoes a strain. A strain is usually due to an external force which elicits internal reacting stresses in the body acted upon. Cytological differentiation is frequently a manifestation of these internal reacting stresses.

It will prove to be an illuminating study to search for the cellular forces outside of the immediate differentiating zone under

observation. This search necessitates lower magnifications in order to enlarge our field of view. Heretofore cytological differentiation has been studied *per se* with magnifications of 1000 to 2000 diameters which considerably reduces our range of view. The higher magnifications are profitable in revealing cytological detail, but the interpretation of the process is lost unless in conjunction with the higher, intermediate magnifications are used. By employing all possible magnifications of the microscope in connection with naked-eye studies we are less likely to lose the forest for the trees. Such a method is likely to reveal the interaction of related developing parts. Before applying this method it will be of advantage to consider briefly the different types of strain with which we are concerned.

DEFINITION AND CLASSIFICATION OF STRAINS

Elastic bodies are those in which a change takes place in the relative positions of their parts in contradistinction to rigid bodies in which no change occurs in the relative positions of their parts. Elastic bodies may suffer changes in their size or shape. Any definite alteration in the form or dimensions of an elastic body is called a strain.

This fact may be brought out in the following illustration: A rod which becomes longer or shorter is strained. Water when compressed is strained. A stone, beam, or mass of metal in a building or in a piece of framework, if condensed or dilated in any direction or bent, twisted or distorted in any way is said to experience a strain. A ship is said to 'strain' if, in launching or when working in a heavy sea, its different parts experience relative motions.

The simplest strain is a linear one. The stretching of an elastic cord is an example. This strain is called homogeneous when every portion of the cord has its length changed in the same ratio, so that the ratio of the initial to the final length of each part is the same as this ratio for the whole. The ratio of the final to the initial length is called the ratio of the strain; it represents evidently the quantity by which the initial length must be multiplied to obtain the final length. The elongation is the

ratio of the change in the length to the initial length. A negative elongation, or shortening, is called a compression. A positive elongation, or lengthening, is called a tension.

When all lines in a body parallel to a certain direction are changed in the same ratio, and no lines perpendicular to these are changed either in length or direction, the body suffers a strain of simple elongation. If, however, a second set of lines at right angles to these also suffer such a change, then there is elongation in two perpendicular directions; and if these lines are all in the same plane, the strain is a surface strain. A square elastic sheet, if the elongation be e in a direction parallel to one edge, and e' parallel to another, will be converted by the strain into a rectangular sheet, the sides of which are proportional to the strain-ratios. Evidently two equal and parallel lines drawn on the square will remain equal and parallel after the change in form; and the strain will be homogeneous. If the elastic sheet be circular, the strain will change the circle into an ellipse, the two perpendicular directions which remain perpendicular after the strain becoming the axis of the ellipse. If these lines remain parallel to their original directions, the elongations take place along them and the strain is called a pure strain. If not, the strain is compounded of a pure strain and a rotation.

As seen above, the principal axis of a strain is the principal axis of the ellipse into which the strain converts a circle. If the increase of length along one such principal axis is equal to the decrease of length along the other principal axis, the strain under these circumstances is called a shear. Evidently in a shear the area of the plane itself remains unaltered. Any plane figure may be converted into a strained figure; that is, the shearing strain may be produced simply by fixing one of its sides, and moving all lines parallel to this fixed side in their own directions, through spaces which are proportional distances from this fixed line. The amount of this sliding motion which takes place between lines which are unit distance apart is called the amount of shear.

When a solid body undergoes a strain, a change may take place in its dimensions in one or more of three perpendicular directions. If the strain is such that all parallel lines within it are altered in

length in the same ratio, the strain is called a uniform or homogeneous strain, as previously pointed out. Thus, for example, a sphere when subjected to strain is converted into an ellipsoid, a solid every plane action of which is an ellipse. This ellipsoid is called a strain-ellipsoid. In any homogeneous strain of a solid body there are three directions at right angles to one another, which remain perpendicular after the strain. These directions are those of the three principal axes of the strain-ellipsoid.

Along one of these directions the elongation is greater and along another less than along any other direction in the body. Along the remaining one the elongation is intermediate. The principal axis of a strain is the principal axis of the ellipsoid into which it converts a sphere. The principal elongations of a strain are the elongations in the direction of its principal axis. According to Thomson and Tait, "Any strain may be viewed as compounded of a uniform dilatation in all directions, superimposed on a simple elongation in the direction of one principal axes, superimposed on a simple shear in the plane of the other two principal axes." With this brief account of the nature of strain we may now pass on to the consideration of the effects of differential growth in intestinal development.

The most rapidly growing part of the intestine is the epithelial tube (figs. 1 to 6). In 10- to 23-mm. embryos the descending colon grows relatively more rapid in diameter than in length. The increase in diameter is due primarily to the rapid growth of the entodermal epithelial tube and only partially to its surrounding mesenchymal cloak. The latter is relatively passive in growth with respect to the former. It is during this early increase in diameter that the inner smooth-muscle coat is in the process of formation. The mesenchymal cells are drawn out gradually in a definite series of concentric rings. These rings appear not unlike those of the planet Saturn and the annular nebula in Lyra.

A definite centripetal force is active in the rapid, spiral growth of the intestinal epithelial tube. The surrounding mesenchymal cells are thrown into a definite series of concentric rings accord-

ing to their various densities. Those possessing the greatest density joining the outer ring in the tangential path of the force, whereas the inner rings will be composed of bodies forming a gradient of decreasing densities. The cells forming the outer ring will be most elongated. Their water content decreases and viscosity increases.

As this concentric initial smooth-muscle layer becomes differentiated it tends to restrict the diametrical growth of the epithelial tube. The epithelial mitotic figures under this restriction shift their planes of division from a right angle to a parallel position with the smooth-muscle cells. This shifting results in an elongation of the intestine.

In embryos 25 to 40 mm. in length, the elongation of the descending colon is more rapid in growth than that of the diameter. It is during this period that the outer longitudinal muscular coat is in the process of formation. The rapid growth of the epithelial tube in length tends to elongate the peripheral undifferentiated mesenchymal cells which were not directly involved in the formation of the inner smooth muscular coat.

The differentiation of the outer longitudinal muscle coat therefore coincides, in time, with the rapid growth in length of the intestinal epithelium. The inner smooth-muscle coat, on the other hand, is formed during the period of the rapid growth of the intestinal epithelial tube in diameter.

In this study, the initial zone of rapid growth is found in the epithelial cells. Kinetic energy is transferred from within to the surrounding splanchnic mesenchyme by rapid spiral expansion of the entodermal epithelial tube. The less actively growing cells of the peripheral region of the intestinal wall are elongated. Later the potential energy of the elongated cells is transferred to those of the epithelium, resulting in a retardation of the growth in diameter. Immediately following this retardation of diametrical growth, the period of rapid growth of the intestine in length takes place. In this development, therefore, the factor of growth motive force, as a cause in the transference of kinetic and potential energy, is definitely detected.

Once the formation of the inner circular muscular rings is fairly established, a resistance to growth in width is encountered by the cells surrounding the rapidly dilating lumen. These cells then grow primarily along the path of least resistance in a longitudinal manner. At this stage the longitudinal muscle cell, spherical in shape in figure 15, is elongated to a spindle-shape structure in figure 16.

In conclusion an interesting correlation in the development of the oesophagus in the human may be cited. This correlation was detected in the work of Jackson ('09) and in that of Keibel and Elze ('08). The former investigator studied the developmental topography of the oesophagus, the two latter the histogenesis of the oesophagus. Jackson states that the descent of the stomach is accompanied by a great elongation of the oesophagus. In a 9.4-mm. specimen the oesophagus measures 1.8 mm.; at this proportion, it should measure 4.3 mm. in an embryo 22.8 mm., but its actual length is found to be 8 mm. The year previously Keibel and Elze reported that the oesophagus in 12.5-mm. embryos show a circular but no longitudinal muscle layer; in 17-mm. embryos they find a circular layer with the longitudinal layer faintly indicated. The histogenesis of the outer longitudinal layer of the oesophagus as studied by Keibel and Elze coincides in time with the rapid elongation of the oesophagus, due to the descent of the stomach, as recorded by Jackson.

GROWTH MOTIVE FORCE IN LIMB DEVELOPMENT

The detailed description of the direct observations made on bone and skeletal muscular development will be reserved for a subsequent communication.

When the embryo is approximately 10 mm. in length, the first indication of the limb is a bud filled with a densely packed mass of uniform mesenchymal cells. Eventually, when the embryo is 14 mm. in length, a condensation of nuclei is detected in the center of the bud. This central condensation represents the primordial blastemal skeleton. It is the most rapidly moving or growing part of the limb. This is evident by the greater number

of mitotic figures and by the relative scarcity of cytoplasm and consequent closely compact nuclei. As the central core of the limb pushes forth more rapidly than that of the peripheral continuous mesenchymal cells, there is a tendency for the latter to be pulled out, stretched, or elongated by the former. The traction force of the rapidly growing appendicular core exerted upon the surrounding mesenchyme is the internal stimulus of a correlated part, resulting in the elongation of the nuclei of the premuscular mass in the direction of the blastemal skeletal growth.

From this direct observation that the cells of the premuscular mass are elongated in the direction of skeletal growth, we detect the objective evidence of the transference of kinetic energy from the zone of rapid growth to that of the relatively passive one. As differential growth continues and the growth motive force becomes more and more manifest, there is also detected a drawing out or stretching of the peripheral syncytial cytoplasm in the direction of the skeletal growth. This is first shown by the appearance of relatively parallel rows of discrete, isolated granules which represent differences in density of the cytoplasm due to the traction to which it is subjected. This is comparable to the tendency of a viscid substance, like egg albumen, to collect in droplets if placed between two glass slides when these are separated by a shearing force.

When the viscosity of the cytoplasm increases, on the other hand, with increased structural differentiation, these granules fuse and form a continuous condensed cytoplasmic strand known as the myofibril. At first this myofibril is coarse, but as the traction of skeletal growth continues it gives rise to numerous fibrils finer in texture. Thus, there is a direct proportional increase of the cytoplasmic components with continued skeletal growth. The formation of the embryonic skeletal muscles represents a definite reaction to the growth of the skeleton. These muscles tend to restrict the growth of the skeleton in length. This is manifested by an increasing condensation of the skeletal core.

This condensation is seen in the transition of the densely nucleated syncytial blastemal skeleton into the cartilaginous skeleton. The greater stability of the latter counteracts the deforma-

tion that would naturally occur in the former as the primitive muscles begin to contract. On the other hand, with increased skeletal condensation there is presented a more rigid base, and this in turn acts as a stimulus to more definite muscular differentiation. This is detected by direct observation in the splitting up of the uniform premuscular masses into its individual muscular components. Muscular forces become consequently more definitely applied and the definitive parts of the skeleton become more clearly outlined.

As the growth motive force of differential growth continues, the musculature becomes too vigorous for the cartilaginous base. The blastemal skeleton, as noted above, is supplanted by the cartilaginous one; there is now found another replacement of the cartilaginous by the osseous skeleton.

The changes which occur in a cartilaginous component of the skeleton, as the femur, in the formation of the more stable bony base, together with the concomitant muscular changes are as follows:

1. There is a bending of the cartilaginous femur with the convexity of the bow directed toward the M. quadriceps extensor. This deformation is incident to the contractility of the thigh musculature and the inception of the adduction action in rotation of the hind limb. This femoral strain is due to active and passive muscular stresses.

2. A strain fibrosis is detected on the weaker convex tensile aspect of the curved femur resulting in the histogenesis of the primary perichondrium which subsequently encircles the shaft.

3. Concomitant with increased muscular differentiation and subsequent activity there is a progressive dehydration, increase of viscosity, and increase of total acidity (table 1).

4. Inception of necrobiosis of the cartilage cells is seen immediately underlying the initial location of formation of the primary encapsulating perichondrium. This necrotic change is due to the diminished blood supply caused by the restricting action of the forming perichondrium. By injection and serial sectioning methods it is revealed that all capillaries and incipient discrete vesicles, precursors of capillaries, are peripherad to the primary perichondrium.

5. The vesiculated cartilage cells are arranged along definite curved tensile and compressile stress lines. Previous to the bending of the femur these cells are irregularly related to one another.

6. Hyalinization of cartilaginous matrix in the central zone of the curved femur is next observed.

TABLE 1

LENGTH OF EMBRYO	TITRATION OF 1 GRAM OF EMBRYONIC PREMUSCLE AND MUSCULAR TISSUE TO $\frac{N}{10}$ NaOH
<i>mm.</i>	<i>cc.</i>
10	2.5
12	3.5
13	3.5
14	4.9
16	9.0
19	11.0
20	13.0
22	14.0
23	13.5
24	13.8
25	17.0
27	23.0
30	21.5
32	24.0
35	27.8
37	31.0
39	32.1
40	31.5
42	34.0
45	35.5

7. Calcification then takes place in the hyalinized matrix. These intergrading steps in the condensation of the matrix is incident to increased muscular growth and functional activity and to the passive resistance of the musculature to skeletal elongation.

8. A subperiosteal osteogenetic and constricting cellular zone is begun immediately underlying the initial zone of fibrosis on the summit of the convexity of the curved femoral rod. This osteoblastic constriction quickly encircles the shaft. This is the

beginning of a consecutive series of bony deposition. This bony deposit is due to two factors: first, the stimulus of the functionally active thigh muscles and, second, the stimulus of the restriction to growth at the ends of the rapidly elongating femoral rod due to passive muscular resistance. These two factors tend to stimulate the formation of the osseous skeleton in replacing the calcified cartilaginous skeleton.

From the foregoing brief account it is desired to emphasize the following:

That there is a direct transference of kinetic energy from the more rapidly growing skeleton to the less actively growing primitive musculature and a reactive transference of potential energy from the latter to the former, tending to a condition of equilibration. With the inception of functional muscular activity there is a direct transference of kinetic energy from this tissue to the growing skeleton tending to retard or alter its motion or growth. The resistance passively manifested by the muscles is an additional factor tending to inhibit skeletal growth. This fact is also noted by Holl, Schomberg, and especially by Bardeen. In this case there is a transfer of potential energy due to position from the muscles to the skeleton. This active and passive play of the muscles on the cartilaginous base resulting in a condensation of a more stable framework and the consequent more definite effect of the latter on the former is due to a direct transference of energy by conduction. This transference of energy is of fundamental importance and is produced by the motive force of differential growth.

SUMMARY

Intestinal development

1. The region of most active mitosis, per mm. of cross-section, in the intestine is the entodermal epithelial tube. The mitotic figures primarily follow a path of a left-handed helix.

2. The region of least active or relatively passive growth per mm. cross-section is the mesenchyme, derived from the splanchnic mesoderm, surrounding the epithelial tube.

3. The rapid expansion due to epithelial growth in a rotating spiral manner of the intestinal lumen is greater than the activity manifest in the surrounding mesenchyme. This causes a pressure in the latter resulting in a flattening and an elongation of the mesenchymal cells. The successive changes in shape of these cells through the spherical, ellipsoidal, and spindle cellular phases are seen. The mesenchymal wall decreases in thickness, due to tension caused by epithelial tubular dilation.

4. The rotating spiral growth of the epithelial cells causes the formation of a series of mesenchymal cellular and fibrillar concentric rings due to the centripetal force of the former.

5. The inner circular smooth-muscle cells are differentiated in the outer more condensed margins of the ring. At these points the developing tensional stresses are greater than within the ring.

6. The tensional stresses to which the elongated strained mesenchymal cells are subjected appear to be a dynamic stimulus to smooth-muscle differentiation.

7. The inner circular smooth-muscle coat is the first one differentiated and is incident to the rapid growth of the epithelial tube in diameter. The kinetic energy of epithelial growth is transferred to the surrounding inner developing annular muscle. The latter soon tends to restrict the growth of the epithelial tube in diameter. The tube, pursuing the lines of least resistance, grows in length. During the period of rapid growth in length the outer longitudinal muscle coat is in the process of formation.

8. There is thus a definite interaction in intestinal development. We find evidence of a transference of kinetic energy from the zone of rapid growth of the epithelial tube to the less active mesenchymal wall resulting in the storage of potential energy due to position in the latter. Subsequently a transfer of resisting potential energy from the elongated mesenchymal cells to the rapidly growing cells of the epithelial tube. This tends to retard growth in diameter and to accelerate growth in length of the epithelial tube.

9. The developing musculature loses water. It increases in viscosity and total titratable acidity.

10. The increase in size of the granules in the mesenchyme is incident to the increase in viscosity. These granules are arranged in rows parallel to the long axis of the elongated nuclei. The same forces at play in nuclear elongation are involved in the formation of the rows of granular fibrils. The formation of the coarse continuous myofibrils occurs at a period when the viscosity and dehydration increases rapidly.

11. The following factors are intimately involved, therefore, in myogenesis:

- a. Tensional stresses elicited by a force external to the differentiating myoblasts.
- b. Loss of water.
- c. Increase of viscosity.
- d. Increase of total titratable acidity.

Limb development

1. The region of most active mitosis, per mm. cross-section in the limb is the skeletal core.

2. The region of least active or relatively passive mitosis, per mm. cross-section, is the surrounding continuous syncytial mesenchyme.

3. Potential energy is transferred from the rapidly growing blastemal skeleton resulting in an elongation or a homogeneous strain of the surrounding continuous syncytial mesenchyme.

4. With the rapid progressive extension of the blastemal skeleton more and more strain is put upon the elongating mesenchymal cells. The latter reacts upon the former continuously. There is a progressive condensation of the skeleton through the embryonal to the alveolar or cellular hyaline cartilage stages. This gradual condensation is detected during a period when the premuscular masses are being split into the individual muscles between 14- and 18-mm. stages.

5. Between 19 and 21 mm. the muscles become functionally active. Limb rotation is begun during this period.

6. The longitudinal continuous myofibrils are differentiated between 14- and 18-mm. stages.

7. As the growth motive force of differential growth continues, the musculature becomes too vigorous for the cartilaginous base. The blastemal skeleton, as noted above, is supplanted by the cartilaginous one; subsequently another replacement of the cartilaginous by the osseous skeleton occurs.

8. There is a direct transference of kinetic energy from the more rapidly growing skeleton to the less actively growing primitive musculature and a reactive transference of potential energy from the latter to the former, tending to a condition of equilibration. With the inception of functional muscular activity there is a direct transference of kinetic energy from this tissue to the growing skeleton tending to retard or alter its motion or growth. The resistance passively manifested by the muscles is an additional factor tending to inhibit skeletal elongation. This fact is also noted by Holl, Schomberg, and especially by Bardeen. In this case there is a transfer of potential energy due to position from the muscles to the skeleton. This active and passive play of the muscles on the cartilaginous base resulting in a condensation of a stable frame work and the consequently increased definite effect of the latter on the former is due to a direct transference of energy by conduction. This transference of energy is of fundamental importance and is produced by the motive force of differential growth.

General deductions from the study of myogenesis

Contractility is a fundamental property of primordial protoplasm. The protozoan, amoeba, possesses the property of contractility in all possible directions. The function of contraction in one definitive direction characterizes muscle tissue from that of undifferentiated and isolated organized particles of primordial protoplasm. What initiates the progressive series of physico-chemical changes in primordial protoplasm resulting in an alteration of its attribute from non-specificity to specificity of direction of contractility? This question is answered as follows:

The primordial protoplasm before differentiating into muscle tissue, must be subjected to a certain minimal homogeneous and

ellipsoidal strain. This strain is objectively evident by an alteration of the form of the spherical nuclei into the ellipsoidal and spindle conditions and by an elongation of the granular cytoplasm into parallel granular and continuous fibrillae. The fibrillae are arranged along lines of internal and reacting tensional stresses. The ends of the primordial protoplasm, in tension, must be attached to supports of which one, at least, is mobile. The tensional stresses are reactions to simultaneous forces extrinsic to the zone of myogenesis. The external forces cause a progressive divergence or separation of the mobile supports to which the primordial protoplasm is attached. Therefore, muscle tissue is not self-differentiating, but is dependent upon an external dynamic stimulus. As regards smooth and skeletal muscles, this stimulus is the motive force of differential growth.

Growth motive force is any agency which tends to produce a transfer of kinetic energy, from an active to a less active group of cells, and of potential energy from a less active to an active group, in a cellular field of differential growth until equilibrium is established.

Whether or not the end-product in muscular formation will be of the smooth or cross-striated type depends upon the intensity of the stimulus of tensional stresses to which the mesenchyme is subjected. The genesis and maintenance of muscle tissue represents a resultant or equilibration of converging factors which are active and formative during development. One of these factors is the tensional stresses to which the mesenchyme is subjected by a force extrinsic to the differentiating zone. In subsequent involution or degeneration of muscular tissue, during the prenatal or postnatal periods, this equilibrium is upset by altering or destroying the tensional reacting stress.

It is a pleasure to record my grateful acknowledgment to my former chief, Dr. H. Von W. Schulte, of Creighton University, for his encouragement, helpful interest and suggestions, and for the opportunities he has extended to me in order to complete this part of my study on bone and muscle development.

I wish also to express my indebtedness to Mr. M. W. Murphy, manager of the Cudahy Packing Company; Dr. O. A. Edwards, private veterinarian and supervisor of the Swift Packing Company, and to Mr. L. A. Orchard, superintendent of the Armour Packing Company, South Side, Omaha, for their courtesies and generous permission in allowing me to obtain unlimited numbers of pig embryos for this study.

For the beautiful clear-cut illustrations, my thanks are due to Madame Helen Ziska.

Finally, for the ever ready help in completing this work, I owe my lasting gratitude to my wife.

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PLATE 1

EXPLANATION OF FIGURES

The tissue was fixed in Zenkers solution; the sections were cut at 8μ and stained with iron-hematoxylin and picric-acid-fuchsin. The drawings were made with the aid of a Spencer camera lucida. Figures 1 to 6 are magnified 100 diameters.

- 1 Transverse section of descending colon 10-mm. pig
- 2 Transverse section of descending colon 14-mm. pig
- 3 Transverse section of descending colon 20-mm. pig
- 4 Transverse section of descending colon 25-mm. pig
- 5 Transverse section of descending colon 31-mm. pig
- 6 Transverse section of descending colon 46-mm. pig

ABBREVIATIONS

<i>dm.</i> , dorsal mesentery	<i>sp.</i> , Meissners plexus (submucous)
<i>cm.</i> , inner circular smooth-muscle layer	<i>ap.</i> , Auerbach's plexus (intermuscular)
<i>lm.</i> , outer longitudinal smooth-muscle layer	<i>sm.</i> , serosa
<i>mt.</i> , mesenteric taenia muscle band	<i>subm.</i> , submucosa
	<i>p.m.</i> , primordial mucosae cells

N. B.—Note especially rapid increase in width of epithelial tube and the absolute decrease in thickness of mesenchymal wall due to tension stresses elicited by the growth of the former.

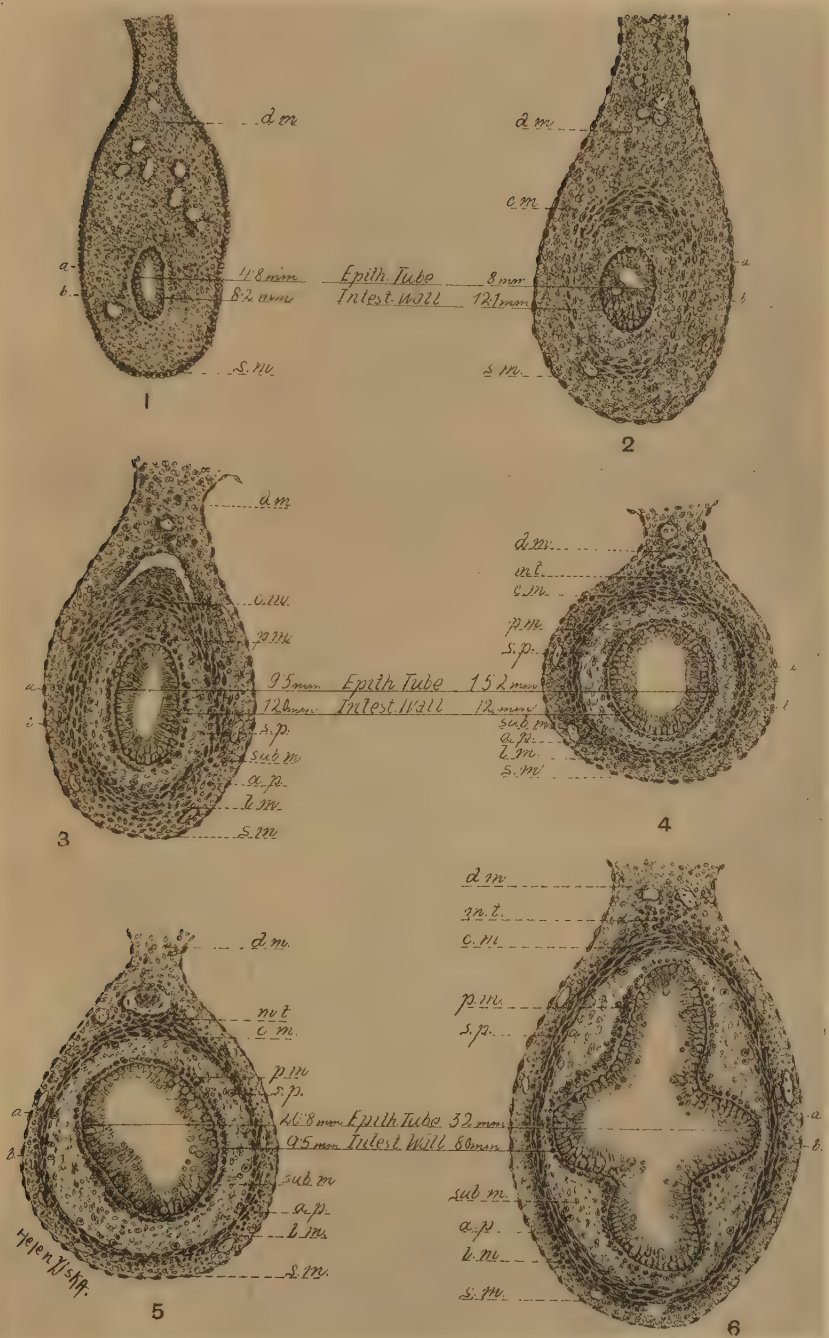


PLATE 2

EXPLANATION OF FIGURES

7 High-power drawing through intestinal wall at region marked *a - b* on figure 1. $\times 800$.

8 High-power drawing through intestinal wall at region marked *a - b* on figure 2. $\times 800$.

ABBREVIATIONS

<i>mit.</i> , mitosis	<i>g.f.</i> , granular fibrillae
<i>b.m.</i> , basement membrane	<i>c.m.</i> , circular muscle nucleus
<i>m.s.</i> , mesenchyme	<i>s.m.</i> , peritoneal epithelium

9 High-power drawing through intestinal wall at region marked *a - b* on figure 3. $\times 800$.

10 High-power drawing through intestinal wall at region marked *a - b* on figure 4. $\times 800$.

ABBREVIATIONS

<i>mit.</i> , mitosis	<i>p.m.</i> , primordial mucosae cells
<i>b.m.</i> , basement membrane	<i>s.p.</i> , submucous nerve plexus
<i>m.s.</i> , mesenchyme	<i>l.f.</i> , longitudinal muscle fibrilla, cross-section
<i>g.f.</i> , granular myofibrillae	<i>a.p.</i> , Auerbach's plexus
<i>c.m.</i> , circular muscle nucleus	
<i>s.m.</i> , peritoneal epithelium	

11 High-power drawing through intestinal wall at region marked *a - b* on figure 5. $\times 800$ diameters.

12 High-power drawing through intestinal wall at region marked *a - b* on figure 6. $\times 800$ diameters.

ABBREVIATIONS

<i>mit.</i> , mitosis	<i>p.m.</i> , primordial mucosae cells
<i>b.m.</i> , basement membrane	<i>s.p.</i> , submucous nerve plexus
<i>m.s.</i> , mesenchyme	<i>l.f.</i> , longitudinal muscle fibrilla, cross-section
<i>g.f.</i> , granular myofibrillae	<i>a.p.</i> , Auerbach's plexus
<i>c.m.</i> , circular muscle nucleus	<i>c.f.</i> , continuous coarse myofibrillae
<i>s.m.</i> , peritoneal epithelium	

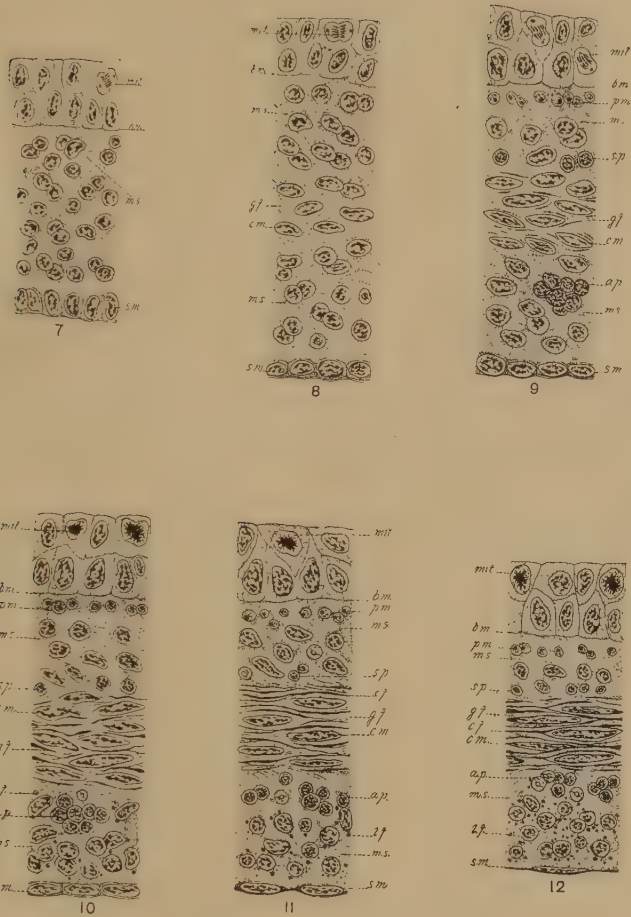


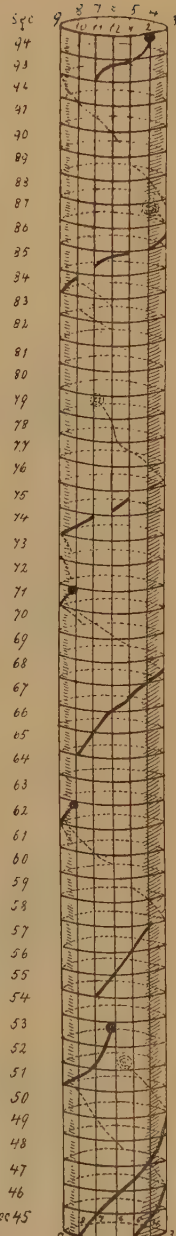
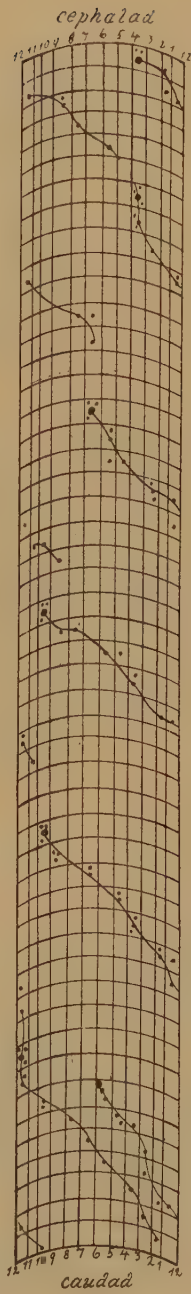
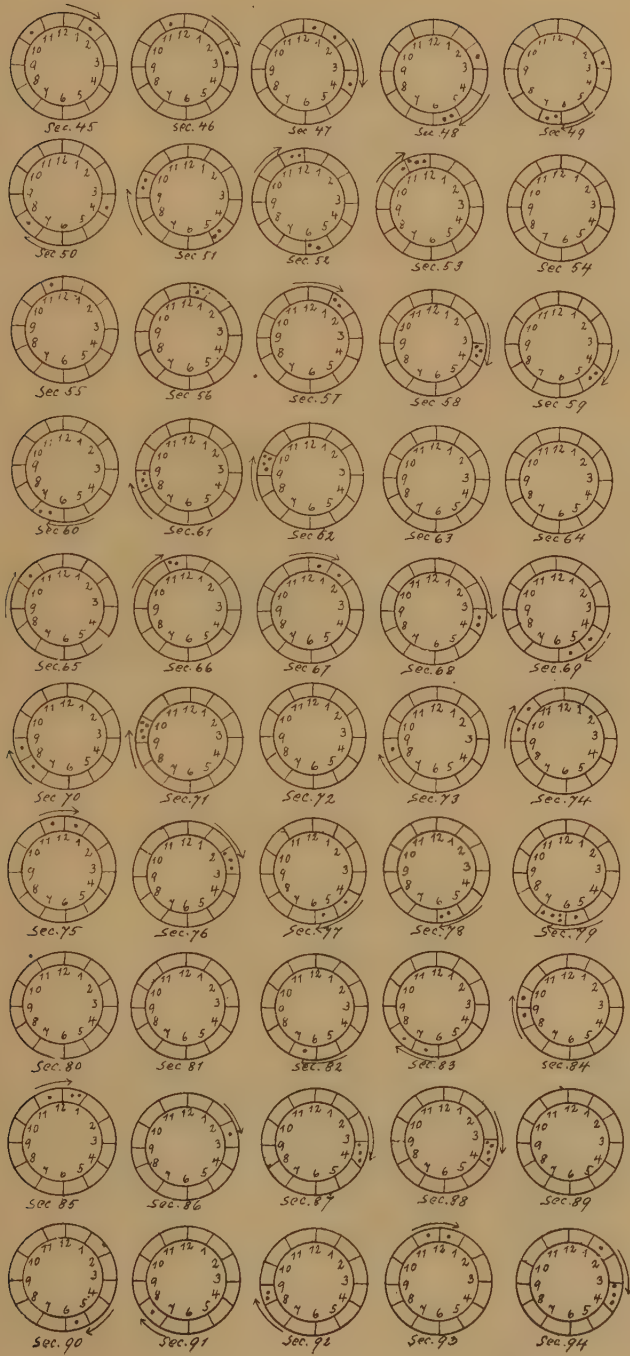
PLATE 3

EXPLANATION OF FIGURES

13 Longitudinal reconstruction of the cross-sections nos. 45 to 94. This figure together with the cross-sections represents a plotting of the exact location of mitosis in the epithelial tube. Figure 13 is depicted as a tube cut through the middorsal region at 12 o'clock and lying flat.

14 Represents figure 13 in graphic reconstruction; the flattened tube is folded up so that the edges of the middorsal cut are in apposition. The spiral paths of the mitotic figures are objectively evident. The apical region of the respective paths are globular. This globular end is always directed cephalad. The basal end of the spiral path is directed caudad. The front and back aspects of the paths, as well as the cylindrical reconstruction is represented by solid and broken lines respectively.

Sections 45 to 94 represent the cross sections of the epithelial tube of descending colon. Section 45 is caudad; 94 is cephalad. The circles are numbered like a clock. Within the area enclosed by the two circles the dots are seen which represent the position and number of the mitotic figures. The arrows represent the direction of the spiral mitotic path which is seen to be right-handed. The predominant path, however, is left-handed. The large intestine of twenty animals was plotted. In only one was the mitotic path found to present a dextro-tropic rotation.



EXPLANATION OF FIGURES

ABBREVIATIONS

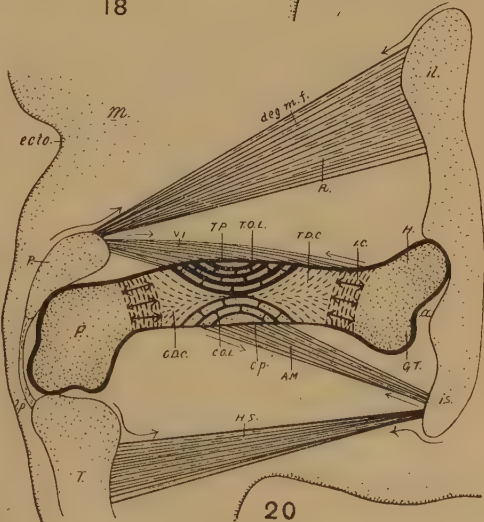
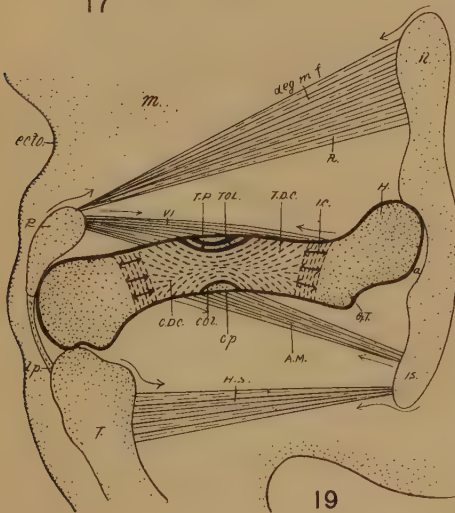
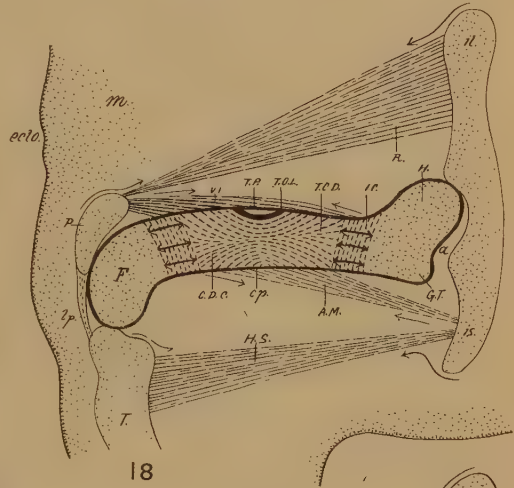
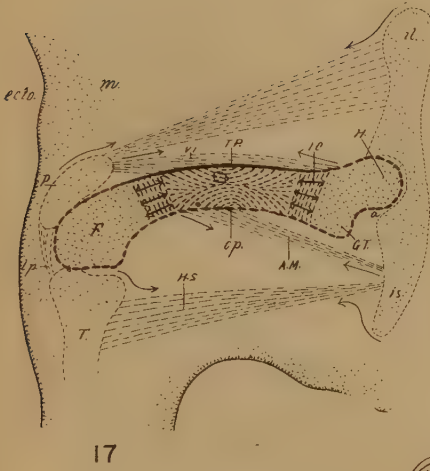
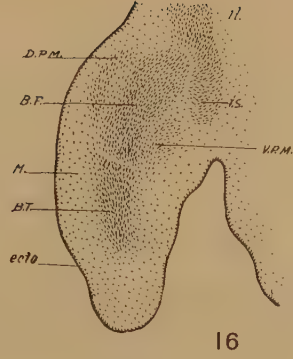
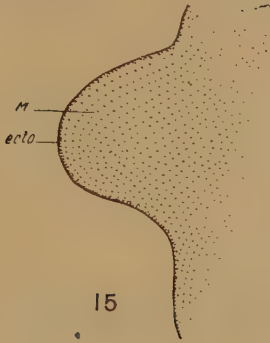
ecto., ectoderm

ABBREVIATIONS

ecto., ectoderm

ABBREVIATIONS

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Resumen por el autor, Oscar V. Batson.
Universidad de San Luis.

Deselectrificación de las cintas de parafina por medio de la
corriente de alta frecuencia.

La cinta de parafina, al separarse de la navaja, con frecuencia se mueve, se adhiere a la navaja o es atraída por los objetos cercanos. Esta dificultad, conocida generalmente como electrificación, es muy molesta cuando se cortan secciones seriadas en tiempo frío y seco. La carga estática es de carácter negativo y está localizada en el tejido y no en la parafina. Esta carga se debe al rozamiento de la navaja sobre el tejido, porque si se corta un bloque de parafina sin tejido contenido en ella, no se produce cinta electrificada. La carga eléctrica puede suprimirse y prevenirse satisfactoriamente ionizando el aire ambiente por medio de un aparato portátil de alta frecuencia del tipo de "rayos violetas." Se frota el microtomo con esmeril, se coloca oropel sobre el soporte de la navaja y se sustituye el electrodo de vacío del aparato de alta frecuencia, por una barra envuelta en oropel. El electrodo de oropel se dispone de tal modo que la descarga de la brocha tenga lugar a través del área que recorre la cinta al ser producida por la navaja. El aparato debe mantenerse en marcha mientras se corte el tejido.

Translation by José F. Nonidez
Cornell University Medical College, N. Y.

DE-ELECTRIFICATION OF PARAFFIN RIBBON BY MEANS OF HIGH-FREQUENCY CURRENT

OSCAR V. BATSON

Department of Anatomy, Saint Louis University.

Electrification of the paraffin ribbon, particularly on the high-speed rotaray microtome, has been responsible for the great difficulties in serial work, particularly in cold, dry weather. Various methods of eliminating the trouble have been tried with indifferent success.

The problem was analyzed, first, as to the nature of the electrification; second, the source and reason for a collection of the charge; third, a means of discharging the electricity as it is formed.

The nature of the charge was determined by means of the electrophorus. The charge on the metal plate of the electrophorus is positive. The electrified paraffin ribbon is attracted to the metal plate of the electrophorus (positive) through a distance of several inches and is conversely repelled by the wax plate (negative). A ribbon possessing no charge is affected but little, so the charge on an electrified ribbon may therefore be said to be a negative one.

The electrification of the ribbon comes about through the friction of the block on the knife and does not occur when paraffin alone is cut. Each section produces a certain amount of frictional electricity, and once a charge is formed, the paraffin as a non-conductor prevents its escape except into the air, and the escape into the air is dependent on the ionization of the gas particles to carry the charge.

The solution for a de-electrification of the ribbon would therefore resolve itself into terms of air ionization to permit a discharge of the electricity as it is formed. This was first attempted by using carnotite at the suggestion of Prof. Hermann Schlundt, of the University of Missouri. A bell jar containing several ounces of radio-active carnotite was placed over the microtome and knife so that the 'active deposit' might accumulate. The

experiment proved unsuccessful, although an electrified ribbon lost its charge in one-fifth the normal time when exposed to carnotite.

The following procedure, however, has proved quite successful. A portable 'violet ray' high-frequency apparatus is employed, substituting for the usual vacuum electrode a rod of wood, 8 inches long, closely wound with wire-cored Christmas-tree tinsel. The idea of using tinsel must be credited to Dr. T. G. Lee, of the University of Minnesota. The apparatus was clamped in position so that the tinsel electrode stood parallel to the knife edge and about 2 inches in front of and above it. Additional tinsel was placed on the block holder and the knife supports. The microtome was grounded to a water pipe. The distance was adjusted to give a brush discharge, i.e., a distance beyond the possibility of a spark discharge, and the vibrator was set so as to give a faint purple glow from the electrode in a darkened room.

Under these conditions, bits of previously electrified ribbon, adhering to the knife support and block, immediately dropped to the table. No electrification of the ribbon occurred with the microtome running rapidly, while the brush discharge was taking place. Curling of the ribbon recurred immediately when the current was turned off. Checking on the electrophorus, it was found that both positive and negative plates were discharged by being introduced into the high-frequency field.

CONCLUSIONS

1. Electrification of paraffin ribbon is due to a negative charge which results from the friction of the tissue on the knife. It accumulates because of an insufficient ionization of surrounding air.

2. The charge can be completely and satisfactorily removed by ionizing the surrounding air with a portable high-frequency apparatus with tinsel electrodes, and grounding the microtome.

3. The distance of the tinsel electrodes must be adjusted to give a faint brush discharge.

4. The stream of the current is through the microtome, and disagreeable sparking to the operator is absent. A slight odor of ozone is neither disagreeable nor harmful.

Resumen por el autor, Henry Bayon.
Universidad Tulane, Nueva Orleans.

Un caso de membrana costocoracoide osificada fusionada con la clavícula.

El sujeto objeto de este trabajo era un varón negro, de musculatura bien desarrollada, y presenta al reflejar el pectoral mayor una placa cuadrilátera de hueso que se articula con el esternón y se extiende lateralmente hacia arriba hasta una distancia de media pulgada del proceso coracoides, con el cual está unido por medio de una banda fibrosa. El hueso está unido con la clavícula, que forma su borde superior redondeado y ensanchado; el músculo subclavio falta y el pectoral menor se inserta en el extremo distal del hueso anormal. La indicación de mi asociado, Dr. Baker, acerca de la posible conexión del hueso descrito con alguna anomalía de la cintura pectoral es probablemente correcta. En la rana toro, *Rana catesbiana*, el hueso coracoides se extiende desde la escápula hasta el esternón y está dividido en dos segmentos: Una ancha placa de hueso debajo, que es el coracoides propiamente dicho, y una barra delgada encima, el procoracoides, que representa la clavícula. En el desarrollo ontogénico de la clavícula de los mamíferos el cartílago en que aparece después el centro primario de osificación se deriva del coracoides primitivo. Por consiguiente, es probable que el hueso anormal hallado corresponda al coracoides primitivo fusionado con sus derivados, es decir, con la membrana costocoracoide y la clavícula. Huntington cita la presencia de uno o dos nódulos cartilaginosos en la membrana costocoracoide. En el sujeto descrito en este trabajo la mayor parte de la membrana costocoracoide (fascia coracoclavicular) y el músculo subclavio se han osificado. Una prueba mas evidente de la identidad del hueso con el ligamento costocoracoides y la membrana es su perforación por la vena cefálica, cuya desembocadura en la vena axilar, es por otro lado normal.

Translation by José F. Nonidez
Cornell University Medical College, N. Y.

A CASE OF OSSIFIED COSTOCORACOID MEMBRANE FUSED WITH THE CLAVICLE

HENRY BAYON

Department of Anatomy, Tulane University

ONE FIGURE

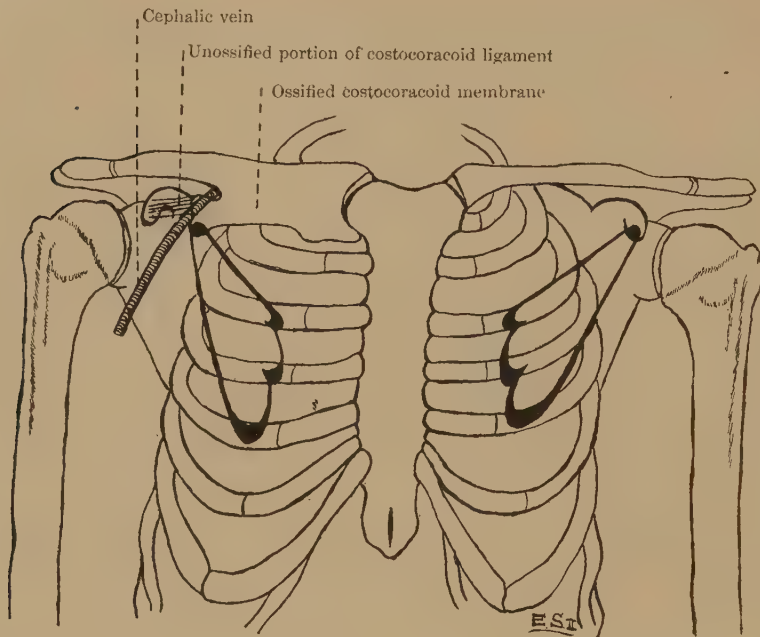
The subject, a negro male, with excellent muscular development, presents after reflecting the pectoralis major a quadrilateral plate of bone articulating with the sternum and extending lateralward to above half an inch from the coracoid process, to which it is united by a fibrous band. The bone is fused with the clavicle, which forms its upper rounded and expanded border; the subclavius muscle is absent and the pectoralis minor inserts at the distal end of the abnormal bone. The suggestion of Doctor Baker, my associate, that the condition might be connected with some abnormality of the pectoral girdle is probably quite correct.

In *Rana catesbiana*, bullfrog, the coracoid bone extends from the scapula to the sternum and is divided into two segments: a broad plate of bone below, the coracoid proper, and a slender bar above, the procoracoid, representative of the clavicle.

In the ontogenetic development of the mammalian clavicle the cartilage in which the primary center of ossification is further developed is derived from the primitive coracoid. It is consequently quite probable that the abnormal bone here found corresponds to the primitive coracoid fused with its derivatives, namely, the clavicle and the costocoracoid membrane.

Huntington cites the presence of one or two cartilaginous nodules in the costocoracoid membrane. In the subject here presented the greater part of the costocoracoid membrane (coracoclavicular fascia) and the subclavius muscle have undergone ossification. A further evidence of the identity of the bone with

the costocoracoid ligament and membrane is its perforation by the cephalic vein, which otherwise normally drains in the axillary vein.



Resumen por el autor, Henry Bayon.
Universidad Tulane, Nueva Orleans.

Diferencias raciales y sexuales del apéndice vermiforme.

El objeto del presente trabajo es el describir las diferencias que existen entre el apéndice del blanco y del negro, las cuales podrían explicar la mayor susceptibilidad para la apendicitis en la raza blanca, si es que existe tal susceptibilidad. Las observaciones efectuadas incluyen diferencias sexuales y raciales en el tamaño, musculatura, número relativo de linfocitos y criptas, y vascularización del órgano. Del examen microscópico de secciones transversales de cien apéndices se deduce que las diferencias mas salientes en las dos razas se refieren al número mas elevado de linfocitos en el apéndice del hombre blanco y la mayor riqueza vascular del mismo órgano en el negro. Las estadísticas del Hospital de Caridad de Nueva Orleans, que fueron consultadas incidentalmente, parecen confirmar una susceptibilidad mayor de la raza blanca a las enfermedades de otros órganos linfáticos, tales como las tonsilas palatinas y faríngeas.

Translation by José F. Nonidez
Cornell University Medical College, N. Y.

RACIAL AND SEXUAL DIFFERENCES IN THE APPENDIX VERMIFORMIS

HENRY BAYON

Department of Anatomy of Tulane University

About thirty years ago the appendix had practically no history, either physiological or pathological.

Howard Kelly, in his extensive work on the vermiform appendix and its diseases, recalls that only in 1824 was the appendix recognized as an organ susceptible to disease arising primarily in its own structure, although mention was made of isolated cases such as Mestivier's recorded in 1759 in which a postmortem examination revealed a pin concealed in the appendix, which had caused inflammation resulting in the death of the patient. This and other similar cases related in Kelly's work show that even in the eighteenth century the appendix was recognized as susceptible to inflammatory lesions, but it was not until 1886 that the appendix was placed in the category of organs susceptible to surgical disease. From that time the daily harvest of appendices has steadily increased. At the beginning of that period we hear Frederick Treves, one of the pioneers of appendectomy, clamoring against the indiscriminate removal of the appendix, which he brands as a needless and illogical recklessness.

Since that time a number of speculative statements have appeared regarding the purpose of the appendix, usually more or less fanciful and sometimes positively grotesque. From the high office of abdominal tonsil we find it elsewhere relegated to the abject rôle of the ordinary mechanical grease cup. In studying the minute structure of the appendix, it is true that large numbers of lymphocyte accumulations are found within its walls, but at best these amount to little compared with similar accumulations found elsewhere in the intestinal canal and are in no way different from the solitary and aggregated lymphatic nodules.

Needless to say that the grease-cup theory finds no support from whatever angle the organ is viewed. It evidently originated in 1749 from an old theory of J. Vosse, who claimed that the glands of the cecum were not sufficient to moisten its contents and that the function of the appendix was to provide additional secretion.

It is not the purpose of the present study, however, to discuss the function of the appendix nor the conditions which call for its removal. It was undertaken with a view to possible differences in structure, both as to race and as to sex.

In considering disease of the appendix, the following questions suggested themselves: Is appendicitis more frequent in the white race than in the negro? Is the disease more prevalent in one or the other of the sexes? And if there are racial and sexual differences, is there anything in the structure of the appendix to account for such differences?

The first question, if records and surgical experience are given consideration, is answered decidedly in the affirmative. The statistics, however, on this, as unfortunately on a great many other subjects, are totally unreliable, even though tabulated intelligently and in good faith.

The eagerness displayed by the medical profession in coming before the public, both in print and in lecture, no doubt in a great many instances with very laudable intent and good effect, places within reach of the more intelligent layman much of the interpretation of his own ills and pains. He seldom ignores the signs and symptoms of appendicitis. As a result, the first tinge of pain in the right iliac region will sound a loud note of warning, followed by a rush to the surgeon, who at once proceeds to remove the appendix, in which postoperative examination frequently reveals little or no inflammatory change. This statement, however, is made with due regard to surgical prudence which takes no chances in a condition where prompt treatment means so much to the patient's safety. At this juncture it may not be inappropriate to refer to the opinion so frequently expressed, that appendicitis is on the increase. That the number of appendectomies has increased there can be no question, but that appendicitis is increasing is more than doubtful.

In contrast with the alertness of the better classes and their readiness to part with an offending organ, is the ignorance and apathy of the poor negro concerning his disease and the counter-indifference of his medical attendant. Acute indigestion or heart failure are convenient and ready forms for his death certificate. Acute gangrenous appendicitis may have caused his death, but his tardiness in seeking medical aid or the lack of interest of his doctor, who comes in when the patient is dying or dead, are in many instances responsible for the error in diagnosis. Hence a possible flaw when records are considered, in passing judgment as to the racial susceptibility to appendicitis.

But if statistics are negative in deciding susceptibility, might there not be some structural peculiarity which would make certain appendices more vulnerable than others? Some time ago, in a casual examination of appendices in the dissecting-room, I was struck with the stout musculature of the negro organ as compared with the flabby membranous appearance of the white appendix. Obviously, a fecal stone or a foreign body would have far less chance of becoming impacted or retained in a robustly muscular appendix with active peristalsis possible than in one whose weaker walls would not only fail to rid the organ of its offending contents, but in consequence of the organ's easier distention would favor the storing up of enormous numbers of pathogenic bacteria.

Hoping to arrive at some tangible facts regarding structure which might cast some light on racial and sexual peculiarities, I have examined 100 appendices and tabulated them according to race and sex. The specimens employed comprised 53 negro appendices, 31 male and 22 female, and 47 white appendices, 11 male and 36 female.

METHOD OF PREPARATION

The appendices were at first fixed in 10 per cent solution formalin, then mordanted in the following fluid:

35 per cent aqueous solution bichromate of potash.....	92
Formalin (40 per cent formaldehyde).....	4
Glacial acetic acid.....	5

The appendices were then imbedded and sectioned in celloidin, stained by Delafield's hematoxylin and counterstained in eosin.

LEVELS AT WHICH STAINED SECTIONS WERE TAKEN

In order to obtain more reliable data, dissecting-room appendices were not considered. Appendices so diseased as to show disorganization or destruction of their tissues were avoided. Only recently removed appendices gathered from autopsies and abdominal operations at Charity Hospital and Touro Infirmary of this city and preserved in formalin solution were used. The material included twenty-five slides of cross-sectioned appendices borrowed from the pathological department of Charity Hospital. Each appendix was measured in length and in width and cross-sectioned two or three times from base toward the apex.

The average length, in all cases considered regardless of race or sex, was 9.2 cm. in seventy-one specimens (table 1) and the average width 6.2 mm. in ninety-eight specimens. The length and width of the 100 appendices were not all available. The length was not mentioned in the histories of the twenty-five Charity Hospital slides, and in four of the specimens prepared by myself part of the organ was missing. The width was taken from the mounted cross-sections in all cases except in two, the specimens having been previously opened by the pathologist for inspection.

Tables 2 and 3 show a sexual difference in favor of the male, giving an average of 9.6 cm. (length) and 6.5 mm. (width) in the male against 8.7 cm. (length) and 6 mm. (width) in the female. tables 4 and 5, the racial difference (in the two tables) show an average of 7 cm. (length) and 6.5 mm. (width) in the white and 11.3 cm. (length) and 6 mm. (width) in the negro.

It may well be objected that in tables 2, 3, 4, and 5 the inferences must be unreliable, the number of cases being too restricted. In table 1, however, which deals with the average length of the appendix, regardless of race or sex, the same objection does not prevail. The slight difference in size between the male and female appendix is all that might have been expected, although that,

TABLE 1
Racial and sexual

	LENGTH	WIDTH
White male.....	9 cases—8 cm.	11 cases—7 mm.
Negro male.....	20 cases—11.3 cm.	28 cases—6 mm.
White female.....	37 cases—6.1 cm.	37 cases—6 mm.
Negro female.....	5 cases—11.3 cm.	22 cases—6 mm.
	71 cases av. 9.2 cm.	98 cases av. 6.2 mm.

TABLE 2
Racial, male

	LENGTH	WIDTH
White male.....	9 cases—8 cm.	11 cases—7 mm.
Negro male.....	20 cases—11.3 cm.	28 cases—6 mm.
	29 cases av. 9.6 cm.	39 cases av. 6.5 mm.

TABLE 3
Racial, female

	LENGTH	WIDTH
White female.....	37 cases—6.1 cm.	37 cases—6 mm.
Negro female.....	5 cases—11.3 cm.	22 cases—6 mm.
	42 cases av. 8.7 cm.	59 cases av. 6 mm.

TABLE 4
Sexual, white

	LENGTH	WIDTH
White male.....	9 cases—8 cm.	11 cases—7 mm.
White female.....	37 cases—6.1 cm.	37 cases—6 mm.
	46 cases av. 7 cm.	48 cases av. 6.5 mm.

TABLE 5
Sexual, negro

	LENGTH	WIDTH
Negro male.....	20 cases—11.3 cm.	28 cases—6 mm.
Negro female.....	5 cases—11.3 cm.	22 cases—6 mm.
	25 cases av. 11.3 cm.	50 cases av. 6 mm.

together with racial differences, would seem to offer no solution to the problem at issue, namely, structural peculiarity bearing on susceptibility to inflammation. The tabulations were simply included as a matter of general interest.

The field which seemed most promising was the microscopic survey of the transverse sections. This consisted in measuring the thickness of the longitudinal and circular muscular tunics expressed in terms of microns together with noting the relative amount of lymphocytes, fat and crypts and the vascularity of each appendix, classifying the specimens into three categories, rich, moderate and poor, as indicated in table 6.

TABLE 6
Based upon 100 specimens

	MUSCULATURE IN MICRONS		LYMPHOCYTES			FAT			CRYPTS			VASCULARITY		
	Long	Circular	Rich	Moderate	Poor	Rich	Moderate	Poor	Rich	Moderate	Poor	Rich	Moderate	Poor
			per cent	per cent	per cent	per cent	per cent	per cent	per cent	per cent	per cent	per cent	per cent	per cent
N. M.—31 C.	247.6	350.8	16	22	62	23	32	45	19	55	26	64	29	7
N. F.—22 C.	270.4	375.3	14	64	22	41	41	18	14	36	50	54	27	19
W. M.—11 C.	270.4	435.9	64	18	18	27	55	18	36	9	65	18	18	64
W. F.—36 C.	241.2	392.8	47	44	9	59	29	12	62	23	15	16	21	73

A glance at the figures disproves the first impression regarding musculature. It is, therefore, quite evident that immunity from appendicitis in the negro, if such exists, cannot be accounted for by a stronger peristaltic wave. Indeed, the measurements show a preponderance of muscular tissue in the white appendix.

The racial and sexual differences in the percentage of fat conform with the general distribution of fat elsewhere in the sexes and in the two races. The negro as a race carries less fat in the average than the white, and in both races the female carries more than the male.

The difference in the number of crypts retained is decidedly in favor of the white appendix. This would seem to indicate less

susceptibility to inflammation. Hence, the study of structure in this particular feature, far from confirming disease statistics, offers decided opposition and is quite suggestive to the reverse.

The difficulty, however, presented by the crypts is offset very singularly by the findings regarding both the lymphocytes and vascularity. In the white appendices, 64 per cent male and 47 per cent female were found rich in lymphocytes, and 18 per cent male and 16 per cent female were found rich in vascularity. Comparing this with the findings for the negro appendix, 16 per cent male and 14 per cent female were rich in lymphocytes and 64 per cent male and 54 per cent female were found rich in vascularity.

In the cases here examined the ratio in the two races between lymphocytes and vascularity is inverted—the richer in lymphocytes, the poorer the vascularity seems a characteristic of the white appendix, whereas the reverse obtains for the negro appendix, in which the scarcity of lymphocytes corresponds with rich vascularity. From the figures the fact stands out that the white appendix is richly lymphatic and poorly vascular and the negro organ just the reverse.

In the white appendix are found two conditions predisposing to inflammation more especially of the gangrenous type—a rich supply of lymphocytes indicating predisposition to inflammation and poor vascularity favorable to gangrenous changes.

It may be objected that since the cases were tabulated regardless of health or disease, the prevalence of the appendices rich in lymphocytes might result from inflammatory action. The objection is met by the fact that, although in some cases operation was performed for appendicitis, in a great many other cases operation was performed for disease other than appendicitis, the appendectomy being performed simply as a matter of prudent routine in anticipation of possible future appendical trouble. But even if on that account, the high percentage of organs rich in lymphocytes found in the white cases be considered of negative value, the fact remains that these specimens show a low percentage of vascularity, and if inflammation alone could suggest increased lymphatic richness, it should also accentuate vascularity, which is quite contrary to the finding.

Racial differences in the appendix suggested that corresponding differences might also exist in other diseases of the lymphatic system. Statistical inquiry into the relative number of tonsil and adenoid disease in the two races demonstrated that in 4759 patients admitted into the Charity Hospital during the first three months of 1917, 2258 were negroes and 2501 were whites. In the 2258 negro cases there were 35 tonsil cases and 8 adenoid cases. In the 2501 white cases there were 95 tonsil cases and 21 adenoid cases.

Table 7 shows that the number of tonsil cases was more than twice as great in the white than in the negro and that the number of adenoid cases was twice as large in the white.

TABLE 7

	TONSIL CASES	ADENOID CASES
2258 negro patients.....	35 (0.015 per cent)	9 (0.004 per cent)
2501 white patients.....	95 (0.037 per cent)	21 (0.008 per cent)

In these tonsil and adenoid cases figures may hold out equivocal interpretation: we are well aware that more whites than blacks are prone to become nervous about health conditions and the same suggestion regarding the advisability of parting with the appendix prevails for tonsils and adenoids. It rests with the specialist whether the organs show sufficient evidence of disease to justify operation and the administration of an anesthetic—always a grave responsibility. Be that as it may, if each tonsilectomy and adenoidectomy means diseased palatine or pharyngeal tonsil, the unavoidable and indisputable inference is that tonsil and adenoid disease is more prevalent in the white than in the negro.

The same Charity Hospital records for the first three months of 1917 show a total of twenty-three negro cases of appendicitis against eighty-five white cases. With due allowance for the doubtful trustworthiness of statistics considered from the standpoint of their face value, it may be safely assumed that when viewed in the light of histological findings above submitted, they

are at least quite suggestive of greater susceptibility of the white race than the negro to appendicitis.

Differences in the lymphatic system of the white and negro races may also be inferred from the findings of Bean and Baker, which appear in the *Journal of Physical Anthropology*, vol. 2, no. 1, 1919, under the title of "Some Racial Characteristics of the Spleen Weight in Man." Over 1500 white and about the same number of negro spleens are considered, showing a decided difference in weight in favor of the white spleen.

These findings are well correlated to those submitted in the present study and seem to prove that the white race is more subject to lymphocytic stasis than the negro.

SUMMARY

1. The musculature of the white appendix is not weaker. Indeed, it seemed slightly stronger than that of the negro.
2. The female appendix is richer in fat than the male.
3. The white appendix is richer in crypts.
4. The white appendix is rich in lymphocytes and poor in vascularity and the negro appendix rich in vascularity and poor in lymphocytes.
5. The average size of the appendix is 9.2 cm. in length and 6.2 mm. in width.
6. The white appendix is shorter and wider than the negro appendix.
7. The male appendix is longer and wider than the female appendix.

HUMAN PARASITOLOGY, WITH NOTES ON BACTERIOLOGY, MYCOLOGY, LABORATORY DIAGNOSIS, HEMATOLOGY AND SEROLOGY, by DAMOS RIVAS, B. S. Biol., M.S., M.D., Ph.D., University of Pennsylvania, Illustrated. 716 pages, W. B. Saunders Company, Philadelphia, Pa. 1920.

EXTRACTS FROM PREFACE

A half century ago medicine was more an art than a science. The doors of American medical colleges stood wide open to welcome all who came as students, and if they showed a desire to learn, possessed enough elementary education to enable them to read their text-book and write their examination papers no questions were asked as to their acquaintance with the physical and biologic sciences.

There was no science of parasitology. Parasites were zoologic curiosities that occasionally intruded into the sphere of medical activity.

Now all has changed. The necessities of commerce have led to such extensive geographic explorations that the entire surface of the earth has been explored and charted. Ethnologic investigators have uncovered the location, life and habits of many formerly unknown peoples.

The general rapid advance of scientific knowledge, especially the progress of physics, chemistry and biology, inevitably reacted upon medicine, stimulating the scientific spirit, demanding research upon its obscure problems, and requiring a new type of student whose preparation for medicine must include at least an elementary knowledge of the collateral and fundamental sciences.

The author has for twenty years interested himself in parasitology and has had the good fortune to have studied in public health laboratories at home and abroad, and to have served on sanitary commissions. After years of teaching he now endeavors to bring together the facts of parasitology in a form suitable to the needs of the student and physician. The following pages reflect his personal experiences and present the facts of the subject in a form sufficiently brief to make it a text-book—the modern tendency is to be encyclopedic—and sufficiently full not to omit any important fact or method.

Resumen por el autor, Carl G. Hartman.
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Los fenómenos del parto en el opossum.

En oposición a lo que se cree generalmente, el embrión del opossum, al final del periodo de gestación, que dura diez días, camina por sus propios esfuerzos desde el orificio vaginal hasta la bolsa marsupial, en la que encuentra la mama. La madre no ayuda al embrión durante su paso desde la vagina a la bolsa, pero le lame para despojarle del líquido coriónico, cuando sale por la vulva. Lo mismo que en el caso de las especies australianas *Perameles* y *Dasyurus*, descrito por Hill, los embriones alcanzan el canal vaginal medio no por los canales vaginales laterales, sino por un túnel que aparece de novo en el tejido conjuntivo situado entre la uretra y los canales vaginales laterales.

Translation by José F. Nonidez
Cornell Medical College, New York

STUDIES IN THE DEVELOPMENT OF THE OPOSSUM DIDELPHYS VIRGINIANA L.¹

V. THE PHENOMENA OF PARTURITION²

CARL G. HARTMAN

The University of Texas, School of Zoology

THE METHOD OF TRANSFER OF YOUNG TO THE POUCH

The literature

So far as the writer has been able to discover, there exists in the literature only one account of the actual birth of any marsupial, notwithstanding the abundance of opossums in America and the variety of all marsupial fauna in Australia. Nor does that foremost of all students of marsupial embryology, Prof. J. P. Hill, refer to this topic, although on one occasion ('00, p. 371) he killed a specimen of *Dasyurus* after "one only of the young had been born." Meigs ('47) and Selenka ('87) examined pouch young of the opossum immediately after birth, but made no observation on parturition.

The single recorded observation referred to is that of Dr. Middleton Michel, of South Carolina ('50), who, on January 28, 1847, witnessed the copulation of a pair of opossums, and fourteen days and seventeen hours later saw the birth of the foetuses. In order to show, however, that Doctor Michel failed to see the actual passage of the young to the pouch, two essential paragraphs on the point at issue are here quoted:

¹ Parts 1 and 2 (History of the early cleavage—Formation of the blastocyst) appeared in the *Journal of Morphology*, volume 27, number 1, March, 1916; and Parts 3 and 4 (Description of new material on maturation, cleavage and entoderm formation—The bilaminar blastocyst) appeared in the *Journal of Morphology*, volume 32, number 1, March, 1919. These four parts may be obtained from the publishers.

² Contributions from the School of Zoology, the University of Texas, no. 143.

The pregnant female was found standing on her hind legs; her body was much bent, and propped up against the corner of the cage; her muzzle in immediate contact with the cloacal opening, which was red, tumefied and distended; a young appeared at the opening, and was conveyed by the mother's mouth to the pouch, or perhaps was rather licked in, as her tongue seemed busily employed within, around and about the pouch.

The young are expelled first into the vaginal cul-de-sac, in which they remain for a short time, on the contraction of which they are forced along the vaginal canals one by one; parturition is thus very much prolonged, owing to the circuitous route which the young are obliged to take, and the delay thereby occasioned between the birth of each is the object of the peculiar modification of these parts in this animal, as it affords the requisite time employed in the conveyance of the young to the pouch and their adaptation to the teat.

It is quite clear from the language of this quotation that Doctor Michel did not actually witness the migration of the embryos and that he merely guessed at the method employed by the mother, since he was not sure whether she used her mouth or her tongue. It will, moreover, be shown below that Doctor Michel was also mistaken in presuming that the young at birth pass out by way of the lateral vaginal canals. The observations recorded below indicate that the marsupial female does not actually transfer the foetuses to the pouch and that Doctor Michel's interpretation, as well as the prevailing notion in accordance therewith, is not borne out by the facts.

Some preliminary observations

A series of observations and experiments during the last four or five breeding seasons of the opossum had enforced the conviction that the young reach the pouch and find the teat by their own efforts and are not placed on the teats by the mother's tongue or lips. Why should it be necessary, one may ask, in the absence of actual observation, to presume such undue skill and sensitivity in the adult when a pure instinctive reaction on the part of the young will suffice?

On several occasions I experimented with newly born pouch young, gently removing them from the teats to which they had firmly attached themselves by means of their powerful tongues.

I quote from my notes in one case (no. 301, experimented upon in the presence of Dr. C. H. Heuser, of The Wistar Institute, January 20, 1917):

Female tied down and pouch opened. Young which were removed from teats crawled about, moving hands alternately, as in swimming. Were able to crawl among hairs and find teats by their own efforts. One specimen, removed three times, found teat each time and three others found teats after wandering about.

These experiments certainly argued strongly in favor of some little independence of action on the part of these 'embryos,' a term that Doctor Meigs ('47) would have us abandon when speaking of these "breathing, sanguiferous, digesting pouch young."

On February 6, 1917, on opening specimen no. 402 under anesthesia, I was surprised to find a collapsed but very vascular uterus, as if birth had just taken place. This proved to be the case, for on removing the animal from the table I found that the entire litter of fetuses had been expelled during the operation. They were mostly still alive, entangled in foetal envelopes and immersed in the foetal fluid. To some of the fetuses the umbilicus was still attached; others were free, but no navel could be seen in any case. None of the fetuses, even after being freed of membranes and liquids, could crawl about, as they were apparently drowned in their own embryonic fluid. It seemed likely, therefore, that the embryos, on emerging from the vagina, need the assistance of the mother to lick away the fluid expelled from them, and this was later verified by actual observation.

Embryos near term were also removed from the uterus, freed of their envelopes, and allowed to crawl about over the mother, which they did for at least fifteen minutes.

On one occasion I removed one uterus three days before term (no. 131), and about the time that birth was to be expected from the remaining uterus I injected some pituitrin subcutaneously, hoping to witness parturition thus brought on. But owing to the fact that abortion had previously taken place, as was afterward learned, only mucus was extruded from the genital orifice.

It is interesting to note, however, that after the injection of pituitrin the female licked out the pouch at frequent intervals, an act which probably always precedes parturition.

The birth of the opossum

Specimen no. 443 was brought to the laboratory February 2, 1920, having been captured uninjured several nights before. She was a healthy female of medium size, and by palpation of the mammary glands, after the method which I have described at another place ('19, p. 24), I recognized her as pregnant and likely to give birth within several days. I removed her to my home, where she was kept under observation night and day, and the success which attended the undertaking is largely due to my wife's enthusiasm and perseverance.

The animal was placed just outside a window in a cage illuminated within by a red electric light, which arrangement was least disturbing to the animal as she was insulated against noises from within the room; the sight of persons moving about in the room caused little response on the part of the animal, but slight noises near the cage startled her greatly.

At 10:30 P.M., February 6, 1920, the animal showed signs of restlessness and soon began cleaning out the pouch, which she did about four times. Then began a short series of spasmodic contractions of the abdominal wall, after which she came to a sitting posture with legs extended. At no time did she stand on her hind legs, as Doctor Michel seems to have observed, for such a position is certainly strained and unnatural. I once had an opossum give birth while she was confined in a burlap sack in which she was carried to the laboratory. In this case it was assuredly impossible for her to stand on her hind legs during parturition.

After assuming the sitting posture, our specimen bent her body forward and licked the vulva; however, her position at this time was such that we could not see the embryos, which very likely passed into the pouch with the first licking of the genital opening. Hence we went to the outside where we could plainly hear her

lap up the chorionic fluid; then suddenly a tiny bit of flesh appeared at the vulva and scampered up over the entanglement of hair into the pouch to join the other foetuses, which now could be seen to have made the trip without our having observed them. Unerringly the embryo traveled by its own efforts; without any assistance on the mother's part, other than to free it of liquid on its first emergence into the world, this ten-day-old embryo, in appearance more like a worm than a mammal, is able, immediately upon release from its liquid medium, to crawl a full three inches over a difficult terrain. Indeed, it can do more: after it has arrived at the pouch it is able to find the nipple amid a forest of hair. This it must find—or perish.

Having now satisfied ourselves as to the manner in which the young opossum reaches the pouch, we etherized the female, hoping still to find some of the embryos within the genital tract. But it happened that we had witnessed the last of the litter make the journey. The pouch contained a squirming mass of eighteen red embryos of which twelve were attached, though thirteen might have been accommodated. The remainder were, of course, doomed to starvation. Even some of these unfortunates, however, held on with their mouths to a flap of skin or to the tip of a minute tail, while several continued to move about.

With the mother under the influence of ether, we now gently pulled off a number of embryos from the teats in order to test their reactions. The teats had already been drawn out from about a millimeter in height to double that length, doubtless by the traction of the embryo itself, for the bottom of the pouch certainly presented a busy scene with each member of the close-packed litter engaged in very active breathing and sucking movements.

One detached young, placed near the vulva, crawled readily back into the pouch. Two or three others regained the teats after some delay, and one wanderer, which lost out in the first scramble, found a vacated teat and attached itself even after twenty minutes' delay, showing that the instinct to find the teat persists for some time. If the skin be tilted, the embryos, can

be made to travel upward and even away from the pouch, for they are negatively geotropic.

For locomotion the embryo employs a kind of 'overhand stroke,' as if swimming, the head swaying as far as possible to the side opposite the hand which is taking the propelling stroke. With each turn of the head the snout is touched to the mother's skin as if to test it out, and if the teat is touched, the embryo stops and at once takes hold.

It is thus apparent that the opossum embryo at birth possesses not only fairly well-developed respiratory and digestive systems, but that it has attained a neuromuscular development sufficient to enable it to find its place in the pouch where food and shelter await it.

The number of pouch young

Most female opossums possess thirteen teats, of which usually only the posterior eleven are functional. I have often found as many as eleven pouch young attached, but only in two cases as many as twelve. Doctor Meigs ('47) on one occasion found thirteen. I have seen litters consisting of fifteen, seventeen, and eighteen newly born young in the pouch, with as few as seven attached to teats, and have removed from pregnant uteri as many as twenty-two normal foetuses near term. Such overproduction with consequent mortality has already been pointed out for the opossum and other marsupials (Hill, '10, '11; Hartman, '19).

Folklore

In the popular mind the generation of no animal is so shrouded in mystery as that of the opossum. From New Jersey to Texas several beliefs are current which it might be well to state at this point.

There is a wide-spread notion that copulation takes place in the nostril of the female and that the 'fruit of conception' is blown into the pouch. This superstition rests upon two observed facts: first, that the opossum penis is dichotomous and, second, that the female licks out the pouch immediately prior to parturition.

Another notion is that the pouch young is organically connected with, or 'grown to,' the teat, in fact so intimately that bleeding results from the forced separation of the pouch young. Doctor Meigs ('47) already showed that this is not the case.

Doctor Meigs mentions and refutes the idea prevailing in his time that the pouch young produces a teat wherever it happens to take hold of the skin in the pouch.

Finally, it is often stated that the marsupial mother pumps milk into the pouch young. Whether or not this is true the writer does not know, but certain it is that from the very beginning the young opossum engages in active sucking movements.

THE PASSAGE OF THE FOETUSES FROM THE UTERUS

As is, of course, well known, the opossum, as a member of the order Marsupalia, possesses two uteri. These do not communicate posteriorly, but open each into a separate shallow cul de sac, on either side of a median partition. Each cul de sac communicates laterally with a loop, the 'lateral vaginal canal' (Hill, '97), which curves laterad, then caudad and mediad, until near the midline the two canals almost touch; and from this point backward they lie parallel until they empty into the 'median vaginal canal' (Hill, '97) or urogenital passage (Owen, '68). The lateral vaginal canals thus resemble two question marks placed face to face; the curved portions lie in the body cavity, the 'stems' are imbedded in the connective tissue of the urogenital strand. The urethra forms a third parallel tube, lying in the midline ventrad to the straight portion of the lateral vaginal canals and emptying with them into the median vaginal canal.

In two Australian species Hill (*Parameles*, *Dasyurus*; Hill, '98, '00) made the surprising discovery that the embryos at birth do not pass out through the lateral vaginal canals, but break through by a cleft-like rupture, the 'pseudovaginal canal,' directly into the median vaginal canal from the culdesac into which the os uteri opens. The new passage is described as a split in the connective tissue, at no time lined with epithelium and containing fragments of foetal membranes together with leucocytes and maternal blood clots.

I have on several occasions demonstrated in the opossum the existence of the pseudovaginal passage discovered by Hill. In specimen no. 402, already mentioned as aborting under an abdominal operation, one could follow a bloody trail direct into the median vaginal canal exactly as Hill had described it. The hemorrhage was less severe in no. 443, the birth of whose young has been described above, but the new passage was easily demonstrable. The organs were fixed in Bouin's fluid and sectioned. The findings are quite in accord with those of Hill. The pseudovaginal canal is seen to be simply a slit in connective tissue between the bladder and urethra ventrally and the caudal ends of the lateral vaginal canals dorsally. In formaldehyde preparations of the organs taken from non-pregnant females such a pseudovaginal passage can with great ease be pushed through; that is, the urethra may very readily be separated from the parts dorsal to it. It appears quite certain that the contraction of the abdominal and the uterine walls is sufficient to force the new passage at the time of birth.

The embryonic envelopes are partly retained within the uterus, a fact already noted by Osborn ('87) for the opossum, and partly scattered along the median vaginal canal. None were found in the lateral vaginal canals either by Osborn or by the writer. It is possible that an embryo may even drag parts or all of its foetal membranes to the exterior, in which case the mother may lick it free; but my only evidence on this point is the presence of the foetal membranes about many of the embryos in the case of one abortion.

The opossum should therefore be added to the list of marsupials which force the 'pseudovaginal canal' at parturition.

One might suppose from this that the lateral vaginal canals would possess a special function. The writer believes with Hill that they function as receptacula seminis, since in the marsupials several days elapse between copulation and ovulation. In the opossum the enlargement of the canal is one of the striking features of the prooestrus period. At oestrus they have attained an enormous size and are filled to turgidity with a thin, lymph-like fluid. Soon after ovulation they shrink almost to the resting

stage and are filled with cheesy masses of epithelial cells, which remind one of a similar phenomenon described by Stockard and Papanicolaou ('17) for the guinea-pig at oestrus.

ADDENDUM

Several months after the foregoing paper had been received by the editor of this journal the writer received a note from Dr. H. H. Donaldson, of The Wistar Institute, in which he stated that he had learned from Dr. N. Hollister, Superintendent of the National Zoological Park, Washington, D. C., of a published account of parturition in *Macropus rufus*, the deer kangaroo. The article in question is in the nature of a communication by the observer, Mr. A. Goerling, to the 'Western Mail,' of Perth, Australia, and was published January 3, 1913. Doctor Hollister's kindness in having the article copied makes it possible to present this interesting account to the readers of The Anatomical Record and thus render it more generally available to zoologists. The accounts of the birth of *Didelphys virginiana*, as detailed above, and of *Macropus rufus*, as reported by Mr. Goerling, are seen to be in perfect agreement on the one essential point, namely, that the young reach the pouch and find the teat by their own efforts and entirely without the assistance of the mother. It would seem, therefore, that this will be found to hold universally among the numerous species of the Marsupialia. The following are Mr. Goerling's notes dated December 19, 1912:

THE BIRTH OF THE KANGAROO³

The question of how the young kangaroo comes into the pouch has long been looked upon as answered. According to observations made, the young is born and placed on the pap by its mother, and this view has been accepted by zoologists.

On the 25th of February, 1906, I had the good fortune to make the most interesting and astounding observation. I had a number of *Macropus rufus* and *M. cervinus* in my possession, caged in various-sized cages. On the morning of the above mentioned date I was attracted by the peculiar behavior of a female *M. rufus*. She refused the feed placed before her; and on seeing blood marks in the cage, I

³The italics are mine.

came to the conclusion that the animal had just given birth to a young one. *She was sitting* in that resting position in which kangaroos can often be seen. The tail passed forward through the legs, thus she was sitting almost entirely on the thick part of her tail. She took no notice of my presence, although not more than three weeks in captivity, and *was busy licking and cleaning herself*. Presently she lifted her head, when I was astonished to see a young kangaroo clinging to the long fur about four inches below the opening of the pouch.

It moved about slowly, very slowly, through the fur upwards, using the arms in its progress, and *continually moving the head from side to side*, thus assisting the upward movement. Nearly 30 minutes were required by the little wanderer to reach the top of the pouch, the last end in a semicircle. During the whole of this time the mother paid no attention to her offspring, *offering no assistance, and leaving it entirely to its own exertions*. She then became restless; and not wishing to disturb her, I moved a short distance away, when she at once started to feed. A little later I paid another visit to her cage. She was sitting upright, the young one had disappeared, but the fur was still bearing evidence of the struggle, a plain visible track leading to and ending on the top of the pouch.

Now I had the explanation of a previous observation, but which I misconstrued at the time. I had a female *Macropus woodwardi*—Woodward's kangaroo—in captivity; and noticing blood stains in the cage, I believed the animal was hurt. I then noticed just such a young kangaroo clinging to the fur below the pouch, and thought the mother by restless movements had dislodged it.

My observation of the 25th of February, 1906, proves that *the new born kangaroo has to look after its own safety and reach the pouch without the mother's assistance*.

The arms of the new born kangaroo are strongly developed, the small hands open and close like a cat's paw, and by these strong little arms and hands the young one is enabled to labour its way to the pouch, the place of safety and nourishment.

The question now presents itself, how can the young, with such a hard and firmly closed mouth, attach itself to the pap? I am convinced that at the time of birth the mouth has a wider opening and is perhaps more elastic than such specimens possess which are found in the pouch of the mother. Once a young kangaroo is removed from the pap, it is unable to reattach itself.

As concluding proof that all newly born marsupials must reach the pouch by their own exertions, I mention that bandicoots, native cats and those very smallest of marsupials, the pouched mice, have the opening of the pouch in a reversed position to the kangaroos and phalangers. I had once in my possession a very small specimen of pouched mouse, having ten young ones in the pouch, each one not bigger than a grain of wheat. Only through the opening of the pouch being reversed are these smallest of born mammals enabled to reach it with safety and without much exertion.

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Resumen por el autor, Frank Charles Mann.

Clinica Mayo, Rochester, Minnesota.

Páncreas accesorio.

En el presente trabajo se describen dos páncreas accesorios hallados en perros. En uno de los casos la glándula aberrante estaba situada a corta distancia distal del ligamento de Treitz, en la inserción mesentérica del yeyuno. La glándula presentaba forma triangular, midiendo $27 \times 20 \times 15$ mm. Poseía un conducto definido que desembocaba en el yeyuno. Su estructura histológica corresponde a la del tejido pancreático normal, pero existe una cantidad relativamente pequeña de tejido insular, y los islotes son muy pequeños.

La segunda glándula aberrante estaba situada en la pared del duodeno, a corta distancia de la entrada del conducto pancreático menor. Presentaba forma de disco y medía 5×3 mm. Su estructura histológica revela la presencia de acini y conductos normales, pero hay una ausencia casi completa de tejido insular. En este último caso es interesante la estrecha relación entre el tejido pancreático y la musculatura lisa de la pared duodenal.

Translation by José F. Nonidez
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ACCESSORY PANCREAS IN THE DOG

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FIVE FIGURES

Many cases of an accessory pancreas in man have been reported. At various times the separate reports have been collected (Opie, Ruediger, Warthin, Wiedman). An accessory pancreas has been found in the wall of the stomach, duodenum, jejunum, and ileum; in a diverticulum of the stomach, jejunum, and ileum; in Meckel's diverticulum, umbilical fistula, mesenteric fat, great omentum, hilum of the spleen, and capsule of the spleen. In some cases the accessory glands have been considered significant clinically in relation to atresia of some portion of the gastro-intestinal canal, obstruction, intussusception, pancreatitis, and malignancy.

From the embryologic standpoint the accessory pancreas has attracted considerable attention and study. The fact that the pancreas arises from two buds and the cells of origin are somewhat scattered seems at least partially to explain the development of accessory pancreatic tissue.

There are few reports of an accessory pancreas in species other than man, although some species are believed normally to have separate pancreatic tissue in the wall of the stomach or duodenum, and the possibilities of its embryologic development in other species are certainly as great as those in man. No reports of an accessory pancreas in the dog were found in the literature.

During two experimental operations on dogs in our laboratory two aberrant pancreatic glands were found. The account of the finding and the description of the two glands follows:

Dog D 93 (experiment 249-19), an adult mongrel bull, weighing 11.7 kg., was being operated on April 30, 1919, by Doc-

tor McQuay for the purpose of developing the technic in some gastro-intestinal operations. While I was demonstrating a method of finding the first portion of the jejunum in the dog, I noted what appeared to be an accessory pancreas just below the ligament of Tritz. Since I was not aseptically prepared to operate at the time, the exact nature of the gland was not determined. The proposed gastro-enterostomy was abandoned, however, and the left ureter was sectioned and anastomosed and the gall bladder removed by Doctor McQuay. The animal quickly recovered from the operation and gained in weight.

July 8, 1919, I explored the animal for the purpose of definitely determining the presence of an aberrant gland (experiment 443-19). The tissue was found to be an undoubted accessory pancreas. Some measurements of the size and position of the gland were taken. At necropsy these were found to be approximately correct. One small lobule, 4 by 2 by 1 mm., of the accessory pancreas was removed and fixed in neutral formalin-Zenker. The major pancreas was examined and found to be normal; one small lobule of it was also removed. Microscopic examination of these specimens showed both to be normal pancreatic tissue.

The animal was kept under observation, as it was planned to study the carbohydrate tolerance and then gradually remove the major pancreas in order to determine whether or not the accessory gland would take care of the carbohydrate metabolism. The animal was pugnacious, and March 5, 1920, was killed in a fight.

The necropsy (107-20) was performed shortly after death. All tissues were well preserved. The site of the accessory pancreas was carefully examined. It was located 32 cm. from the pylorus, 11 cm. below the upper attachment of the ligament of Tritz and 5 cm. below its lower attachment. The gland was roughly triangular, with the small side of the triangle attached quite firmly to the jejunum. It measured 27 mm. along the greater side of the triangle, 20 mm. along the opposite side, and 15 mm. across the small side attached to the jejunum. It was 6 mm. thick. It appeared to be composed of perfectly normal pancreatic tis-

sue. A small duct, extending from the middle of the side attached to the jejunum, passed through the jejunal wall. This duct measured 2 mm. in diameter and 5 mm. in length. On the jejunal side the duct emptied into the lumen of the intestine through a small opening.

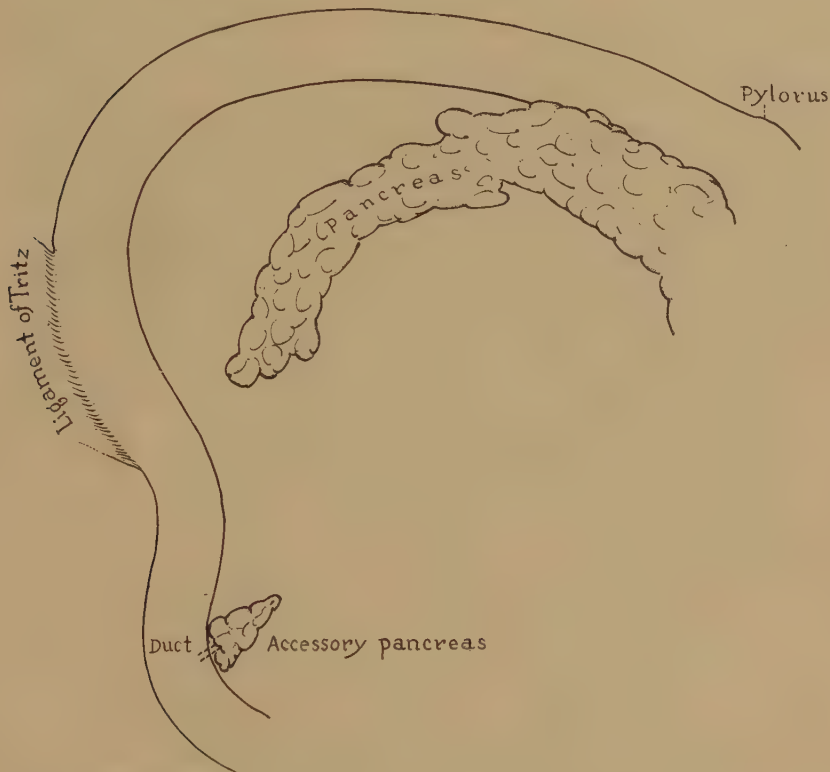


Fig. 1 Diagram showing the relative position of the accessory pancreas of dog D 93.

The major pancreas was large, weighing 45 gm. The animal was found to be normal except for a small lymphoma in the spleen, measuring 6 mm. in diameter.

Microscopic examination of many sections of the accessory pancreas showed it to be composed of normal pancreatic tissue. The acini appeared perfectly normal. A large number of islands

were scattered throughout the gland; it was noticed, however, that the islands were very small. In most instances not more than a dozen island cells were found in one group in a section. In comparison with the islands of the major pancreas they appeared very small indeed. Other than this decrease in island tissue and particularly in the size of the islands, no difference



Fig. 2 Drawing of the accessory pancreas in its relation to the jejunum and the mesentery in dog D 93.

was noted between the major pancreas and the accessory gland (figs. 1 to 4).

Dog D 563 (experiment 200-20), a mongrel black and white hound, weighing 20.4 kg., was operated on March 26, 1920, for the purpose of making an Eck fistula. On pulling up the duodenum an accessory pancreas was found 6 cm. from the pylorus on the right side of the duodenal wall; and 3 mm. above the entrance of the minor pancreatic duct into the duodenal wall, making it about 0.5 cm. from the mesenteric border on the right side. The accessory gland was disk-shaped, 5 mm. in diameter,

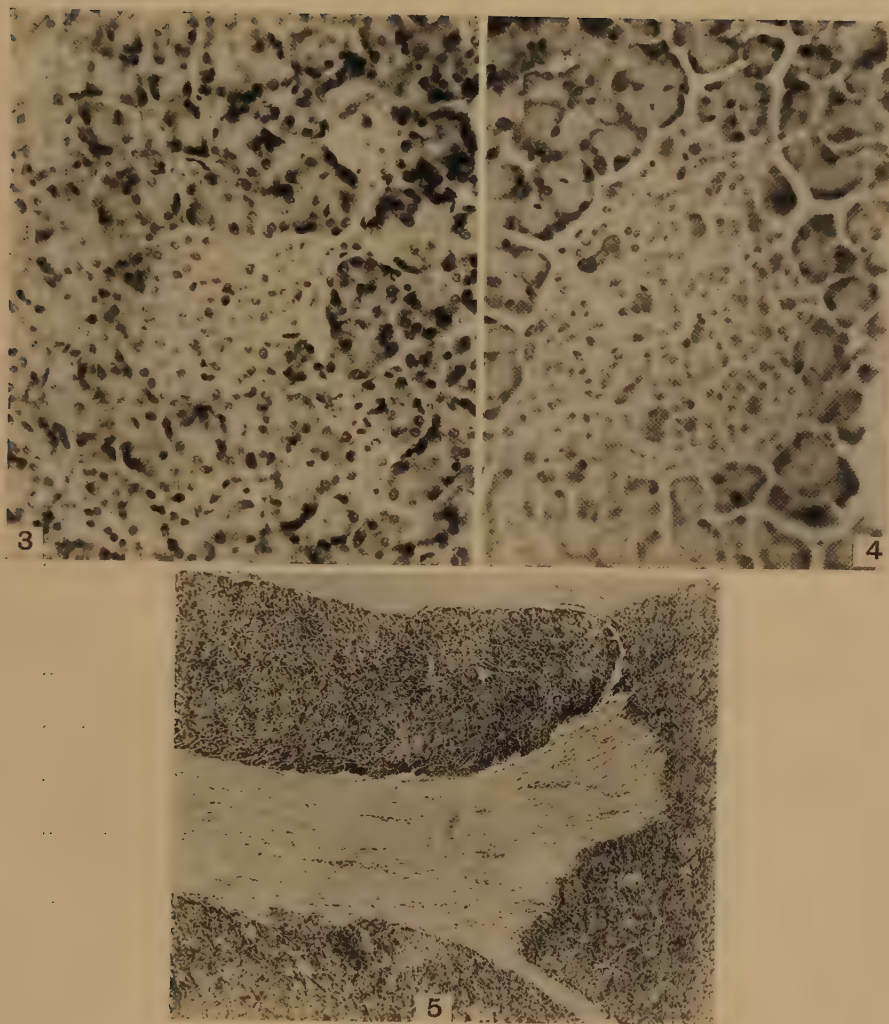


Fig. 3 Photomicrograph of the largest island found after a search through many sections of the accessory pancreas of dog D 93. It is normal, but small. $\times 250$.

Fig. 4 Photomicrograph of one of the average-sized islands of the major pancreas of dog D 93. Compare with figure 3. $\times 250$.

Fig. 5 Photomicrograph of section of accessory pancreas of dog D 563. Note the absence of island tissue and the intimate relation of pancreatic and smooth muscle tissue. $\times 75$.

and 3 mm. thick. It was covered completely with serosa and imbedded in the muscularis, but was quite easily dissected out. It was impossible to determine grossly whether or not a duct connected it with the duodenum. The tissue appeared to be perfectly normal. A specimen was excised and fixed in formalin, and a specimen taken from the major pancreas just below the accessory gland was also fixed in formalin.

On microscopic examination the major pancreas was found to be normal, and several sections of the accessory gland showed this also to be normal pancreatic tissue. Very little island tissue was found. Scattered in various parts of the section were groups of a few, seldom more than six, of what appeared to be island cells. The gland had well-developed ducts; undoubtedly a duct connected it with the lumen of the intestine. The pancreatic tissue and smooth muscle tissue were intimately associated; prolongations of one dipped, finger-like, into the other (fig. 5).

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Resumen por el autor, H. L. Wieman.
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Observaciones relativas al desarrollo temprano de la glándula
suprarrenal humana.

Embrión de 9 mm. 1. Las crestas suprarrenales se extienden posteriormente desde las membranas pleuroperitoneales hasta las crestas genitales. 2. El único indicio de vascularización del tejido suprarrenal está representado por algun corte transverso de un capilar. 3. En la región suprarrenal los ramos comunicantes se extienden ventralmente mas allá de los ganglios prevertebrales del simpático, en forma de fibras nerviosas en apariencia desprovistas de células nerviosas. 4. Las células germinales extraregionales se presentan diseminadas en las proximidades de las crestas genitales.

Embrión de 12 mm. Las glándulas suprarrenales están claramente separadas de los tejidos que las rodean. 2. La región central de la glándula es una red muy vascularizada, cuyos vasos sanguíneos poseen paredes endoteliales bien distintas. 3. El lado medio de cada glándula está en íntimo contacto con la prolongación ventral del ramo comunicante y masas de células ganglionares. Algunas de estas aparecen entre las fibras de la porción distal del ramo, a lo largo del cual parecen emigrar desde los plexos celiacos y viscerales.

Translation by José F. Nonidez
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OBSERVATIONS IN CONNECTION WITH THE EARLY DEVELOPMENT OF THE HUMAN SUPRARENAL GLAND

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TWO PLATES (NINE FIGURES)

The purpose of this contribution is to call attention to certain details in connection with the development of the human suprarenal gland, because they happen to be clearly illustrated in the material at hand. This material consists of two human embryos, nos. 1 and 4 of the author's collection, which were obtained some years ago, freshly killed and fixed, from Drs. H. L. Woodward and Charles Goosmann, of Cincinnati. No. 1 had been killed in a bichromate-acetic mixture, and no. 4 in Bouin's solution. The former measured 9 mm., crown-breech, and the latter 12 mm. Both measurements were made in 85 per cent alcohol after fixation, so that the sizes of the living embryos were somewhat larger than these figures. The embryos were embedded in paraffin, cut into serial sections of 10 μ thickness, and stained on the slide with Delafield haematoxylin and orange G according to the method of Morris ('09). Mitotic figures abound in both embryos, but the fixation is somewhat better in no. 1.

OBSERVATIONS

Embryo no. 1, 9 mm. The suprarenal glands are not recognizable as distinct organs, but consist of a thickening in the mesenchyme on either side of the root of the mesentery, forming a pair of broad ridges projecting into the body cavity from the dorsal body wall. Anteriorly these suprarenal ridges are continuous with the dorsal portions of the pleuroperitoneal membranes, while posteriorly they blend with the genital ridges. Laterally

each is separated from the mesonephros by a distinct groove (fig. 1). Occasionally a transverse section of a blood capillary can be seen in the center of each ridge, the beginning no doubt of the central vein of the adult organ.

The ridges are made up of mesenchyme which shows no evidence of differentiation. The ramus communicans divides into two at the level of the sympathetic ganglion where one of the branches terminates, the other passing ventralward into the mesenchyme. The cells composing the sympathetic ganglia stain more deeply than the surrounding cells, but beyond this they show no appreciable differentiation. The ganglia lie on either side of the aorta somewhat dorsal to it. The nerve strands (axis cylinders?) are easily distinguished and followed, owing to the fact that they stain readily with orange G. The ventral branch of the ramus communicans, which is really the direct ventral continuation of the latter, loses itself in the mesenchyme of the suprarenal region. It seems to be unaccompanied by nerve cells (fig. 3). From the picture one gets the impression that the nerve fibers are pushing their way through the mesenchyme, blazing, as it were, a track along which the ganglion cells are to follow later.

In the posterior part of the suprarenal ridge, the genital ridge, the subepithelial region of the mesonephros, and in the mesentery, one finds large cells with clear cytoplasm and standing out distinctly from all cells (fig. 3, 4, 5). These I take to be germ cells (primary genital cells). Their wide extraregional distribution indicates that these cells undergo a rather extensive migration before reaching the germinal epithelium. This of course is in keeping with what is known about the early development of germ cells in other vertebrates.

Embryo no. 4, 12 mm. The suprarenal glands in this specimen are distinctly marked off from the surrounding tissues (fig. 2). Each one lies with its dorsal surface against the pleuroperitoneal cushion, while in close contact with its median side are bundles of nerve fibers and ganglionic clumps. Near the ventral border, as shown in figure 2, some nervous tissue is pushed into the substance of the gland, but only to a very slight extent, definite

immigration, according to other authors, not taking place until a much later period.

The prevertebral sympathetic ganglion is now a very distinct mass of cells clearly differentiated from the mesenchyme. Its relation to the ramus communicans is somewhat different from that described for the 9-mm. embryo. There is no longer any evidence of a branching in the ramus communicans at the level of the ganglion, the latter lying more directly in the path of the ramus. The ventral extension of the ramus (fig. 1) now passes directly ventralward from the ganglion (fig 2, *v.r.*). Among the nerve fibers of the ventral extension of the ramus can be seen two kinds of cells: 1) those distinguished by a long narrow outline with nucleus of the same shape, which are probably sheath cells and, 2) large irregular cells with yellowish cytoplasm drawn out into processes and possessing rounded nuclei. The latter are undoubtedly migrating nerve cells (fig. 7). They are larger and differ otherwise in their appearance from the nerve cells found in the prevertebral ganglia (fig. 6), but are practically identical with the large nerve cells partially embedded in the ventral border of the suprarenal gland (figs. 2, 8). Comparing the pictures presented by figures 1 and 2 it would seem that in the latter stage the nerve cells are in the actual process of migrating ventralward along the paths marked out by the nerve fibers, which alone are present in the former stage. If some of these migrating nerve cells are destined to enter the gland to form its chromaffin tissue and others to pass on to form the ganglia of the coeliac plexus, there is no way in the preparations at hand of distinguishing the two kinds. According to Soulié ('03), the penetration of the cortical portion of the suprarenal by the parasympathetic cells commences at the 19-mm. stage, which is of course considerably older than the one dealt with here.

The cells of the gland itself are arranged in the form of a branching network penetrated with blood-vessels, and resembling the zona reticularis of the adult organ. A distinct endothelium forms the walls of the capillaries (fig. 9). The only other indication of differentiation in the gland is the ingrowing of connective-tissue trabeculae at the periphery.

DISCUSSION

His, Jun. ('91), described a preliminary nerve-fiber framework laid out in the form of rami communicantes, along which the sympathetic cells wander to form the ganglia. Streeter (Keibel and Mall, v. 2, p. 149) states that in human embryos the migrating cells can be recognized in advance of the loose strands of the tip of the growing nerve which extend through the mesenchyme toward the aorta, and that by the time a well-defined nerve trunk is established, the sympathetic cells have already completed that part of their migration, and the cells then found on the nerve trunk are sheath cells only.

In the 9-mm. embryo under discussion the nerve fibers forming the ventral extension of the ramus communicans beyond the sympathetic ganglia (fig. 1) may have been preceded by a migration of ganglion cells through the mesenchyme, but my preparations do not show nerve cells either among the fibers or at their distal ends (fig. 3). On the other hand, in the 12-mm. embryo the cells found scattered along the course of the fibers are undoubtedly nerve cells rather than sheath cells. I am therefore inclined to believe that some at least of the ganglia migrate to their final location along paths formed of nerve fibers. The well-known work of Harrison ('06) which shows very conclusively that ganglion cells of amphibian larvae develop axis cylinders as outgrowths of the cell body, strengthens my conviction that the nerve fibers forming the pathway develop originally as outgrowths from cells located in the cord. Whether the nerve cells subsequently found among the nerve fibers come directly from the spinal ganglia or from the prevertebral ganglia is another question. I can only say that the migrating nerve cells are larger and differ in outline from those found in the prevertebral ganglia.

As has been noted above, Soulié ('03) states that the penetration of the parasympathetic cells into the cortical portion of the suprarenal gland commences at the 19-mm. stage. Zuckerkandl (Keibel and Mall, v. 2, p. 173) states that the elements of the migrating cell masses, which are entirely or for the most part chromaffin-forming cells, are sharply distinguished from the

neighboring cortical cells by their smallness and intense stain. In my preparations one cannot say with certainty whether such cells are present or not. Deeply staining cells occur bordering the nerve strands and the ganglionic masses, and these may represent the chromaffin cells, but if so they are sharply defined from the nerve cells and are more distinctly epithelial in character.

Zuckerlandl (Keibel and Mall, v. 2, p. 171) found that the suprarenal glands are already vascularized in a 9-mm. embryo, whereas in my specimen of this age the only indication of vascularization is the occasional appearance in the suprarenal ridges of a cross-section of a blood capillary, which simply means that my embryo is younger than his, though both are the same length. In the 12-mm. embryo of my collection delicate endothelial capillaries form a very rich vascular network involving practically all of the gland except the cortical region. The central vein is not visible.

Hoffmann (93) and others have shown that the primordial germ cells are distinct from the elements making up the germinal epithelium of the gonad and that they exist a long time before the appearance of the latter. More recently, Swift ('14) has traced the history of the primordial germ cells of the chick from their origin in a specialized region of the germ-wall entoderm just at the margin of the area pellucida. These cells are carried by their own movement and later by that of the blood to all parts of the embryo and vascular area until in embryos of twenty-six to twenty-nine somites they are found in the splanchnic mesoderm near the radix mesenterii. With the formation of the gonad they gradually pass to that organ. Fuss ('11) describes extra-regional germ cells in a human embryo aged four weeks. He finds them in the mesentery directly under the peritoneum, but not in the germinal epithelium. According to his description, they are large cells of rounded outline, with clear cytoplasm and distinct nucleus. The cells measure 19 to 20 μ in diameter and the nuclei 12.75 μ .

In my 9-mm. embryo, which is somewhat older than the one studied by Fuss, I have found cells resembling the one pictured

by Fuss in his figure and corresponding in every way to those described in his text, except that the measurements I have made are somewhat less than his. Likewise I find the distribution of these primitive germ cells to be somewhat wider than he found, and in my preparations some of the cells have approached very close to the germinal epithelium (fig. 4). The 12-mm. embryo did not prove favorable for the study of these cells, so that I have no data on the range of distribution at this later stage. My observations on the 9-mm. embryo corroborate the statements of Fuss, which indicates that the germ cells of man like those of other vertebrates are characterized by period of migration in the early part of their history.

SUMMARY

9-mm. embryo

1. The suprarenal ridges extend from the pleuroperitoneal membranes posteriorly to the genital ridges.
2. The only indication of vascularization in the suprarenal tissue consists in an occasional cross-section of a capillary.
3. In the suprarenal region the rami communicantes extend ventrally beyond the prevertebral sympathetic ganglia as nerve fibers apparently free of nerve cells.
4. Extraregional germ cells are found widely scattered in the neighborhood of the genital ridges.

12-mm. embryo

1. The suprarenal glands are distinctly marked off from surrounding tissues.
2. The central region of the gland is in the form of a network, and is highly vascular, the blood-vessels having distinct endothelial walls.
3. The median side of each gland is in close contact with the ventral prolongation of the ramus communicans and masses of ganglia cells. Some of the latter are found among the fibers of the distal part of the ramus along which they seem to be migrating to form the coeliac and visceral plexuses.

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DESCRIPTION OF FIGURES

Figs. 1 and 2 are camera drawings made at table level with Zeiss ocular 2- and 16-mm. objective. The remaining figures were made with Zeiss ocular 4- and 2-mm. objective. All figures have been somewhat reduced in reproduction.

ABBREVIATIONS USED IN FIGURES

<i>b.v.</i> , blood-vessel	<i>p.c.</i> , pleuroperitoneal cushion
<i>e.c.</i> , endothelial cell	<i>s.g.</i> , prevertebral sympathetic ganglion
<i>g.c.</i> , primordial germ cell	<i>s.r.</i> , suprarenal ridge
<i>g.r.</i> , germinal ridge	<i>v.r.</i> , ventral continuation of the ramus communicans
<i>n.c.</i> , nerve cell	
<i>n.f.</i> , nerve fiber	

PLATE 1

EXPLANATION OF FIGURES

- 1 Transverse section through suprarenal region of 9-mm. embryo.
- 2 Transverse section through suprarenal region of 12-mm. embryo.
- 3 Enlargement of portion of ventral continuation of the ramus communicans of figure 1.
- 4 Enlargement of portion of germinal ridge of figure 1, showing a primordial germ cell near the germinal epithelium.
- 5 Enlargement of portion of subepithelial portion of the suprarenal ridge of figure 1 also showing a primordial germ cell.

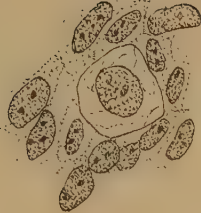
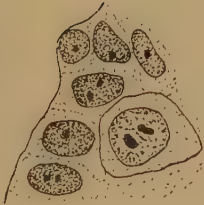
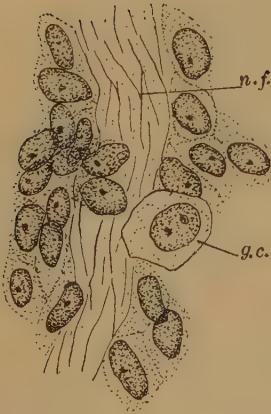
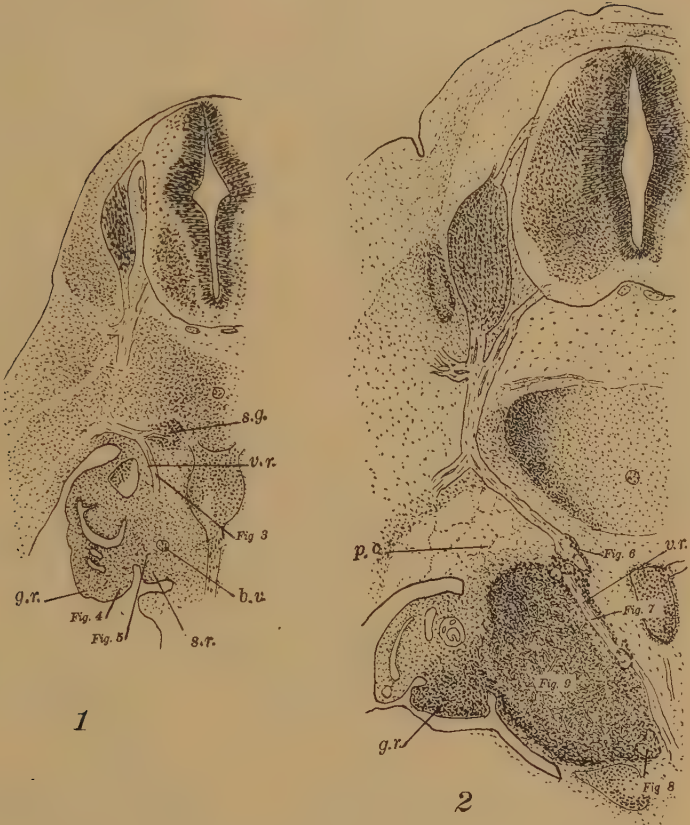


PLATE 2

EXPLANATION OF FIGURES

- 6 Enlargement of portion of the prevertebral ganglion of figure 2.
- 7 Enlargement of the ventral continuation of the ramus communicans of figure 2.
- 8 Enlargement of the ganglionic mass embedded in the ventral border of the suprarenal gland of figure 2.
- 9 Enlargement of the central portion of the suprarenal gland of figure 2, showing the capillary structure.



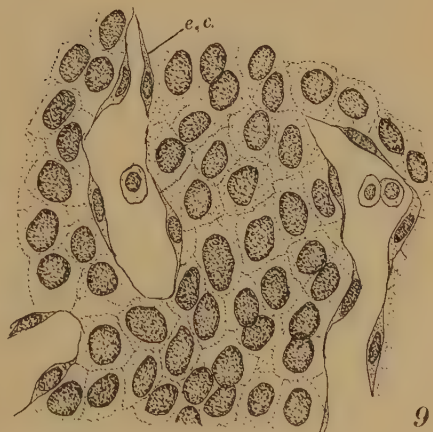
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Resumen por los autores, George B. Wislocki y Tracy Jackson
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Nota sobre la anatomía de las áreas postremáticas.

Las áreas postremáticas son masas de tejido situadas en el extremo caudal del cuarto ventrículo; están compuestas de células de neuroglia y están muy vascularizadas. Al fusionarse forman el techo del canal central de la médula. Están cubiertas de delicadas células endimarias aplanadas, que difieren del epitelio que tapiza interiormente el resto del cuarto ventrículo.

En las áreas postremáticas del hombre se han hallado células nerviosas, designadas con el nombre de núcleos postremáticos. En los animales no se han encontrado células nerviosas en estas regiones. La rica vascularización de estas áreas es un hecho descrito repetidas veces. Los vasos provienen de las ramas piramidales de las arterias cerebelosas inferiores. No se sabe nada acerca de la significación funcional de estas estructuras. Las áreas postremáticas se tiñen intensamente con los colorantes vitales, y este hecho es sorprendente si se tiene en cuenta que todas las demás partes del sistema nervioso central, con excepción de la hipófisis, no se tiñen vitalmente. La coloración de las áreas puede explicarse por la acumulación de moléculas del colorante en las células del tejido conjuntivo situadas en las vainas de los vasos sanguíneos.

Translation by José F. Nonidez
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NOTE ON THE ANATOMY OF THE AREAE POSTREMAE

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The earliest investigators of the behavior of the benzidine group of vital dyes were impressed by the fact that the normal central nervous system remained unaffected by these substances. The choroid plexuses alone were deeply stained, and it was thought that they were responsible for the failure of the dye to enter the cerebrospinal fluid. The only portion of the brain which was observed to stain grossly, aside from the choroid plexuses, was the hypophysis. The dye appeared in this organ principally in the pars anterior.

On examining the tissue of the brain under the microscope, it was discovered, however, that it is not absolutely devoid of stain, since granules of dye-stuff were occasionally discovered in connective-tissue cells of the meninges, in the adventitial sheaths of the cerebral vessels, and in the capsule cells of the spinal ganglia. In the true nerve elements vital-dye granules were never observed under normal conditions.

On examining the brains of a variety of animals after repeated injections of trypan blue we noticed in the gross two bilateral areas at the caudal end of the lateral walls of the fourth ventricle which were quite as deeply stained as the adjacent choroid plexus. These areas were found vitally stained in several monkeys besides in a series of dogs, cats, and rabbits, so that there remained no doubt as to the constancy of the phenomenon (figs. 1, 2, and 3). No mention has been made of the behavior of these areas by either Goldman (1, 2, 3) or MacCurdy (4), to whom we are indebted for our knowledge concerning the distribution of vital dyes in the central nervous system. A possible reason why this staining may have been overlooked by Goldmann is that he worked upon mice and rats in which the areas would necessarily be very

minute. In the species of large animals studied by us the areas could hardly fail to attract attention. An investigation of the anatomy of the caudal end of the fourth ventricle showed these spots to be the *areae postremae*.

The lower end of the *calamus scriptorius* is only briefly described in most text-books of neurology, but it has been the object of special study in the human brain by several investigators, particularly Blake (5), Wilson (6), and Streeter (7).

The *areae* or *eminentiae postremae*, so named by Retzius, are paired mounds of loose, vascular tissue which overlies the caudal third of the *nucleus vagi* and protrude into the lumen of the fourth ventricle. At their superior extremities the areas lie just ventral to the line of attachment of the choroid tela. Caudally they converge and eventually fuse in the midline to form the roof of the central canal. A tiny pocket, the *suprapostremal recess*, exists, as Blake has observed in many animals, between the roof of the central canal and the roof of the ventricle or the *obex*.

Wilson (6) has described and pictured the variations which occur not infrequently in this region in the human brain. In some specimens he noted that the *areae postremae* fuse to form the roof of the central canal. In these instances a *suprapostremal recess* is formed, as in animals, between the *areae postremae* and the *obex* above. In other specimens, however, the areas fail to coalesce in the midline, and consequently the *obex* forms the dorsal wall of the central canal at its emergence into the ventricle. In the latter cases the *eminentiae postremae* are seen in section as bulgings in the lateral walls of the mouth of the canal.

In serial sections the minuter relationships of the areas may be observed. Near their upper poles they appear as low elevations projecting into the rhomboid fossa, bounded mesially and below by the *alae cinereae* and extending laterally to the line of origin of the *taenia*. Midway between their poles, in the region of their greatest development, they appear as two prominent masses bulging into the lumen of the ventricle and overlying the dorsal nuclei of the vagus nerves. A band of dense neuroglial tissue, the so-called *funiculus separans* of Retzius, is conspicuous in

this region. It separates the areae postremae from the alae cinereae which lie beneath and mesial to them. In sections taken farther back, it may be observed how the areae postremae gradually converge and finally fuse, enclosing a space between them and the ventricular floor, the orifice of the central canal. The entire surface of the areae postremae is covered by a delicate, flattened epithelium, and differs in this respect from the rest of the ventricle which is covered by cuboidal or columnar ependyma. The tissue of which the eminentia postrema is composed, consists of a loose network of neuroglia through which runs a rich plexus of arterioles and capillaries. The arterioles are surrounded by perivascular sheaths composed of connective-tissue cells. In addition to the vessels, fibroblasts, and neuroglia cells which were observed by Streeter (7) and Blake (5), the presence of neurones has been described in human material by Wilson (6). He suggests that these nerve cells be designated the 'nucleus postremus.' He also states that Stilling used the term 'Accessoriuskern' to designate the area postrema, and that the latter observer may therefore have been aware of the presence of nerve cells in that region. We have confirmed Wilson's observation in several human brains, but have been unable to find nerve cells in preparations from any of the animals which we have examined.

The embryology of the area postrema has occasioned some discussion. Blake, who is apparently the first writer to investigate the subject, believes that it is part of the remains of the secondary rhomboid lip of His, in common with the obex and the ligula. As we have seen, however, the eminentia postrema is quite distinct from both these structures, which Blake's own illustrations also show. In his figure 28, the area postrema, marked 'secondary rhomboid lip,' is some distance mesial to the attachment of the velum. Elsewhere in the same paper, Blake speaks of the primary rhomboid lip as fusing to "produce a bridge of nervous matter over the emergence of the myelocoele into the fourth ventricle," which is doubtless the interpostremal fusion in this region. Wilson's conception seems much more tenable. He considers the area postrema as a part of the alar lamina of His.

We have studied two human embryos from the Harvard Embryological Collection. In the younger of these, a specimen of 40 mm., the area postrema could barely be made out as a spot of loose, undifferentiated neuroglia tissue, covered with flat ependyma, at the point of emergence of the central canal into the ventricle. In the other, an embryo of 78 mm., the eminentia postrema was perfectly distinct, and displayed all the characteristics of form and structure which mark the adult area, even containing a few nerve cells. In both specimens, the area was at a considerable distance from the roof of the ventricle. In the older one the heaped-up epithelium of the rhomboid lip was to be seen, entirely distinct from the flattened ependyma of the area postrema mesial to it.

The vascularity of the eminentia postrema has attracted the attention of all observers. Haller (8), in his paper on the comparative anatomy of the rhomboid fossa has described its vascular connections. It is supplied from the pyramidal branch of the inferior cerebellar artery (first described by Duret) by three or four long, slender, anastomosing trunks. The principal arteries run along the outer border of the area, and send many arching arterioles transversely across it, from which a plexus of capillaries drains into a set of venules along its mesial edge. The vessels of the eminentia postrema have no connection with those supplying the choroid plexuses and the velum. The blood supply of the areae postremae in the dog's brain is illustrated in figure 4.

We have sectioned the calamus region in a number of vitally stained animals (one monkey, two dogs, two cats, and a rabbit in serial sections) and have examined the areae postremae. Trypan blue was the vital dye employed. Its distribution was alike in all the species. It was observed to occur abundantly as blue granules in many of the connective-tissue cells of the 'adventitial cell' type which invest the small arterioles and capillaries of these richly vascular areas. Particles of dye were rarely observed in the endothelium of the vessels. None was found in the neuroglia cells or in the nerve elements of the adjacent ala cinerea. It is interesting that these areas are the only intrinsic part of the central nervous system which possesses sufficient mesodermal tissue to stain deeply with vital dyes.

Repetition of some of Weed's (9) experiments, in which a solution of potassium ferrocyanide and iron-ammonium citrate was introduced into the ventricles, failed to demonstrate any absorption in the region of the areae postremae.

The abundant blood supply of the areas, the behavior of trypan blue toward them, and the fact that they are covered by an extremely low ependyma raises the suspicion that the areae postremae have some function in the transmission of fluid from the blood stream into the cerebrospinal fluid. The further elucidation of this point would be extremely interesting.

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PLATE 1

DESCRIPTION OF FIGURES

1 Dorsal view of the medulla of a rabbit with the roof of the ventricle removed showing the choroid plexuses and the interior of the rhomboid space. The animal has received repeated injections of trypan blue. The choroid plexuses and the areae postremae are deeply stained.

2 Medium sagittal section of the same specimen.

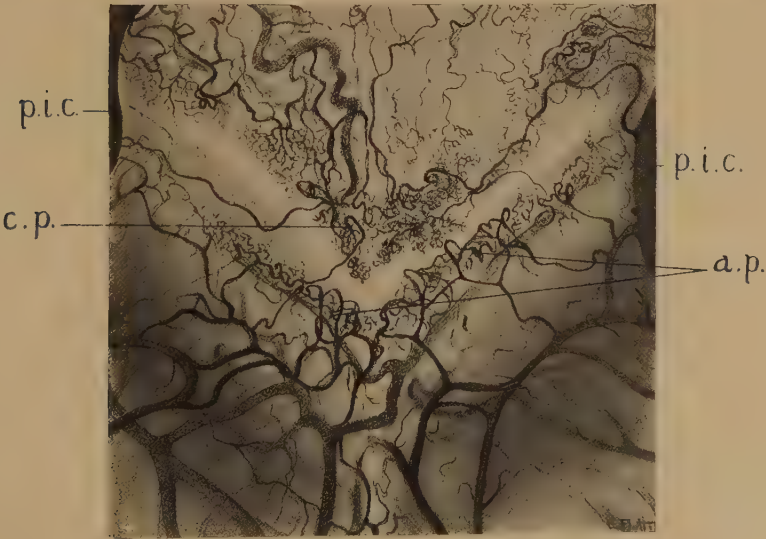
3 Cross section through the area postrema on the right side.

4 The blood vessels of the calamus scriptorius of a dog injected with india ink. The rich anastomosis of blood vessels in the areae postremae is clearly shown.

a.p., areae postremae

c.p., choroid plexus

p.i.c., posterior inferior cerebellar arteries



Resumen por el autor, Alexander Petrunkevitch.
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La unificación de la microfotografía.

La microfotografía puede simplificarse y al mismo tiempo hacer la mas científica por un proceso de unificación de los aparatos. Para obtener este fin todas las partes del aparato microfotográfico deben disponerse de un modo especial. Después de esto deben prepararse tres tablas de datos, conforme se indica en el texto, una de ellas para los aumentos, la otra para los factores de exposición y una tercera para los factores relacionados con los filtros de rayos luminosos.

El uso de estos cuadros abrevia el tiempo de trabajo y la pérdida de material, eliminando todos los errores fluctuantes y dándoles valores permanentes. De este modo se aumenta considerablemente la eficacia del aparato. Las mejores combinaciones de placas y filtros para rayos han sido determinadas mediante pruebas y se describen para un cierto número de coloraciones sencillas y dobles de uso común.

Translation by José F. Nonidez
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STANDARDIZED MICROPHOTOGRAPHY

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ADVANTAGES OF STANDARDIZATION

While the trend of the manufacturer has always been to introduce as much standardization as possible into his methods of production, the scientific investigator has held strangely aloof from anything that might restrict the freedom of his individual effort. The reason for this lies in a partial misconception of the principle of efficiency as applied to science. The feeling of aversion for any standardization has been carried so far that freedom in the selection of methods and the consequent desire to avoid any limitation in the use of apparatus are causing the loss of more time than one would like to admit. None would nowadays expect a photographer to make his own plates or paper. Sensitizing plates to various rays or increasing their rapidity in the laboratory would be futile, for one can obtain on the market the desired product. At the same time the majority of microphotographic apparatus are made on the principle of a universal tool, to be used as it may please the photographer at the time, who sets up or dismounts the apparatus on every occasion when he works with it. The intensity of the light may be increased or diminished by an almost endless combination of adjustments in several parts, such as the source of light, the substage, the diaphragms, the rayfilters; the desired magnification may be obtained by the use of the one or the other combination of oculars and objectives; objects may be photographed with the camera in an upright or a horizontal position, etc. What is the result? Not only a tremendous loss of time due to constant rearrangement of the apparatus and to measuring of the magnification, but an unavoidable variation in the quality of the negatives

and an utter impossibility of duplicating negatives or of obtaining identical magnification after the lapse of a few days or even hours, if the apparatus has meanwhile been deranged.

The latter statement may seem like an unwarranted assertion to anyone who has not had sufficient experience in photographic measurement. Yet, unfortunately, it is quite true. In figuring the magnification, especially when it comes to higher powers, it is practically impossible to determine with absolute accuracy when the scale is focused, and the possible error is quite sufficient to make an appreciable difference in size. It means simply this, that within given limits there is always an error in the stated magnification and that this error cannot be overcome by practical means. But in standardizing the individual apparatus as will be explained below, we can fix the error so that it always will remain the same. If we were to make photographs of a long series of sections we would have at least the same magnification in every case, while under other circumstances the error itself would present a variable.

To be practical, the methods of standardization not only have to accomplish their purpose, but must be simple. Some books give long formulas, the application of which is troublesome and does not give reliable results. A certain amount of derangement in the apparatus will always be unavoidable. If we are to use complicated mathematical calculations every time we want to obtain a given magnification, we defeat our own purpose. From the point of view of theory, the methods of standardization applied by me may appear perfunctory; from the point of view of results obtained, they leave nothing to be desired. They do not remove the errors themselves, but the sources of errors, by making errors constant. And they allow of very rapid work of high quality. At the Osborn Zoological Laboratory where I have worked out the method of standardization and used the apparatus for considerable time, we are able to make a fine negative of any microscopic slide stained by one of the forty-odd stains commonly in use here and at any of the thirty-five different magnifications ranging from 12 to 3000 diameters, without making any calculations or measurements whatsoever except a simple multiplication

of two factors given in special tables. We are able to turn out a finished negative in less time than it would take to find the necessary extension of the bellows for the desired magnification and we can change from one given magnification to another in a few moments. Should the apparatus for some reason have to be temporarily dismantled, it can be again reset, although this of course would take considerable time. The maximum of efficiency is attainable only through fixation of parts.

CHOICE AND ARRANGEMENT OF APPARATUS

Not every microphotographic apparatus is suited for standardization. There are several essentials without which standardization becomes impossible. These are: a rigid bed consisting of one unit; a source of light of permanent intensity; graduated scales for all mobile parts; a set of rayfilters of permanent colors and known wave-lengths. An examination of the majority of microphotographic cameras made by the leading manufacturing concerns of all countries has shown that very few, indeed, may serve the purpose. Thus the largest cameras made by both Zeiss and Leitz in Germany are as if intentionally constructed in such manner as to preclude standardization. Of the British cameras, that made by Baker comes up to the requirements; while in this country the same may be said of the large horizontal camera manufactured by the Bausch & Lomb Company, that model which does not allow the raising of the bellows into a vertical position. As described in their catalogue, the camera has one very important defect which, however, the manufacturers remedy on request, and this is a single holder for rayfilters instead of two, as is imperative whenever one has to use monochromatic light of highly limited wave-length. With this correction and with additional scales engraved on parts of which I shall speak below, the camera proved to be quite suitable for the purpose in question.

A few words about the microscope may be in place here. The stand must be of a regular microphotographic model. From a practical point of view, the choice of lenses at present is largely

a matter of taste. We use Apochromats 16.0, 8.0, 4.0 and oil immersion 2.0. The best oculars to be used are so-called projection-oculars 2 and 4 as manufactured by Zeiss, since they give a flatter field. For small magnifications the micro-tessars are best. When they are used in place of an objective, the sub-stage has to be removed. If possible, the microscope should be with sliding objective changers instead of a revolving nosepiece. These changers are made so as to allow the adjustment of the objectives to cofocal length. There have to be as many changers as there are lenses, and the lenses once screwed in and adjusted should not be again removed, as that would result in an appreciable change of magnification. For the same reason the stand must never be removed from the support to which it has been fastened, nor must the centering be deranged. This necessitates examining the microscope slide for the part to be photographed in a rather awkward position with a consequent loss of time. The difficulty may be overcome by a special construction allowing the replacement of the microscope in the identical position after its removal for the purpose of focusing. But in absence of such a contrivance, the removal of the stand is not permissible under any circumstances. Correct centering of the microscope requires a great deal of time, much more than the loss due to inconvenience in focusing. The support for the microscope is also movable along the bed, and when the microscope has been once centered it becomes necessary to record the exact division on the scale of the bed at which the support has been fastened. This gives a guaranty that in case the apparatus has been dismantled, it may again be assembled without any change in the values of the tables.

THE LIGHTING SYSTEM

Whatever the source of light and the system of condensing lenses, the intensity of light must remain the same for a given record. With other words, the lighting system must be of such a kind as to allow exact recording and returning to each given combination within the shortest time, without any measurements or calculations whatsoever and in the simplest manner possible.

This can be accomplished only if every movable part is provided with an arrow or a pointer and its position recorded on a corresponding immobile scale. If the source of light be a carbon arc, it is best to select once, by experimenting, the most satisfactory distance of the arc from the lens and mark the position of the carbon-holder by means of a transverse line scratched or engraved on the immobile bed of the holder. Still better, to make a ring of a flat strip of heavy copper and rivet it in such a position that the arc is in the correct position when the carbon-holder abuts against the copper ring. This precludes all mistake, is easily done, and requires nothing but the commonest tools. The arc light as furnished by the Bausch & Lomb Company, even under such circumstances, is not a permanent source of light, but the variation in intensity, if the arc is watched, is not sufficient to impair seriously the quality of the work.

All diaphragms must be graduated, for which purpose it is best to measure the diameter of the opening at full stop and engrave lines showing when the diaphragm is closed to one-half its diameter, to one-fourth its diameter and so on. The diaphragms of the microscope must also be graduated in the same manner.

It is absolutely indispensable that the position of the microscope substage should also be recorded. For this purpose the arm carrying the substage should be graduated. That position in which the substage is brought as far as possible toward the objective is most conveniently designated as the zero of the scale, and the scale itself may be metric or English or quite arbitrary, provided the divisions are well marked. Even, bright illumination is obtained by placing the substage condenser in the position which gives critical illumination, and which may be more or less easily found by racking the substage nearer toward or further away from the objective. What is desired in practice is the simultaneous focusing of as many structures of an object as possible. In a photomicrographic instrument provided with a complete condensing system, such as used in the Bausch & Lomb apparatus, this so-called 'depth of focus' is most easily increased by racking the substage away from the objective. The optimum position of the substage may be judged by an examination of the

image of a slide on the ground-glass. Any further increase in the distance of the substage will result in a decrease in light intensity and loss of definition. The optimum position of the substage is different for every objective. The lower the magnifying power of the objective, the greater will be the distance of the substage from the objective. Once the optimum position has been determined for every objective, it must be recorded.

HOW TO PREPARE A TABLE OF MAGNIFICATIONS

The first step in the preparation of a table of magnification is the choice of magnifications desired. If the oculars used are of the common compensation kind, the determination of magnifications is so simple that any number of magnifications may be recorded. All one has to do is to determine the position of the ground-glass carrier for two magnifications at the extreme ends of the bed, let us say for 100 and 500 diameters. The intermediate positions may be derived by a simple calculation, remembering that for a given optical system the magnification is in direct ratio to the extension of the bellows.

The use of projection oculars precludes, however, the application of such a simple method. These oculars are supplied with a correction scale which must be used if the oculars themselves are used at all. The 'raison d'être' of such oculars is their greater flatness of the field which is obtainable only by the use of the correction scale. Zeiss furnishes a formula which may be used to find the necessary correction for a measured extension of the bellows. Unfortunately, there are two reasons why such a procedure is inapplicable in the case of a standardized instrument. First, it requires in every case the measurement of the extension of the bellows and, second, the magnification itself is changed by the adjustment of the correction scale. With other words, if we were to prepare a magnification scale by the method used for common or compensation oculars, we would find, on correcting the field of the projection ocular, that this has resulted in a change of the magnification and that to obtain the desired magnification we have to measure it instead of simply setting the bellows to a given scale. This means, therefore, that the preparation of a

magnification table for use with projection oculars is not a simple process of calculation and requires careful measurements.

It is most convenient, therefore, to select a list of magnifications which are most desirable and which will prove to be sufficient in the majority of cases. The next step is to find the proper position of the bellows for each magnification given, for each combination of objective and ocular. This can be done by the use of a stage micrometer, such as furnished by any reliable optical company, and an exact millimeter scale by means of which the image of the micrometer scale on the ground-glass may be measured. After the bellows have been extended to give approximately the desired magnification, the projection ocular is corrected by the turning of its graduated disc until the edge of the visible disc of light on the ground-glass is quite sharp. This position is recorded in the table. Next the carrier of the ground-glass is moved nearer or further away from the microscope until the millimeter scale shows that the desired magnification has been obtained. Of course, the micrometer scale must be in focus. The position of the ground-glass carrier on the bed may now be recorded. If it is difficult to decide when the micrometer scale is in focus, the process may be repeated several times and the mean of the observations used for the record. It is tedious work, but it pays in the end, because it need never to be repeated. In the table, corresponding with each magnification two figures should therefore be given, one showing the position of the correction disc in the projection ocular and the other the position of the ground-glass carrier on the bed. Such a table naturally has value only for the given combination of stand, objective, ocular, and bed, and would be of no use if reproduced here. Each manufacturer, however, following these instructions, could easily prepare and furnish such a table for a standard equipment.

In preparing the table of magnifications one must bear in mind that the objectives give best definition at a given length of the tube, usually 160 mm. The use of a revolving nosepiece requires the extension of the microscope tube to only 145 mm., because the nosepiece itself measures 15 mm. The use of slid-

ing changers requires an extension of only 140 mm., because the changers measure 20 mm. Should the extension become deranged during the work, the magnification value would also change. To prevent this in the most efficient way, a ring should be made from a strip of flat copper and placed permanently on the microscope tube. The width of the ring may be made of the correct size by filing it down until the tube is in its proper position when firmly moved against the ring. Once placed on the tube, the ring should be left there permanently.

In my table I have twelve vertical columns, each for a different combination of objective and ocular. The magnifications are given in a special column on the left of the table. Each vertical column has two subdivisions, one for the ocular correction, the other for the ground-glass carrier. The figures of each column interlap with the figures of the next column, because the same magnification may be obtained by the use of two or three different objectives and oculars with an increase in the length of the bellows, thus permitting a choice of the most suitable combination in each individual case. For example, if definition is most important, the immersion lens may be used with a lower ocular and shorter extension of the bellows. Where, on the other hand, depth of focus is more important than definition, the same magnification may be obtained by using an 8-mm. objective with a more powerful ocular and longer extension of the bellows. If for some reason, after having examined one combination, one is not satisfied with the result as shown in the image on the ground-glass, it takes but a few seconds to change the combination and to try out several other combinations for the same magnification. Imagine what labor it would entail if we had no table by which to go in such a case!

HOW TO PREPARE A TABLE OF EXPOSURE FACTORS

Only in very rare instances microphotographs can be made without the use of rayfilters. Since the object of a microphotograph, barring a few exceptions of which I shall speak later, is to show as much detail as can be obtained, it is absolutely neces-

sary to know the best combination of rayfilter and plate to be used in each individual case. It would be possible to prepare a single table from which one could find not only this combination, but the necessary exposure in seconds for each given magnification. But such a table would require so many vertical and horizontal columns, that it would defeat its own object of simplifying the procedure. It is quicker to find two factors, one in each of the two small and simple tables, and to compute the necessary exposure by a multiplication of these factors. This can be accomplished if one of the tables shows the exposure factors for all given magnifications without any rayfilter and the other shows the factors for all combinations of plates and rayfilters.

The relative speed shown for dry plates in various photographic manuals and exposure meters naturally refers only to exposures in daylight with a common photographic camera and a lens of a given aperture and focused on infinity. I have compared and controlled several of these tables, and having selected the most important brands of plates am giving here, for the convenience of the reader, a table showing the relative exposure factors or speed of such plates, assuming that the speed of the Standard Orthonon plate equals 1.

Relative exposure factors or speed of photographic plates in daylight without rayfilter

Regular plates

Cramer's Crown.....	1
Marion Record.....	$\frac{1}{4}$
Seed Graflex.....	$\frac{1}{4}$
Seed 27 gilt edge.....	$\frac{3}{4}$
Seed 30.....	$\frac{2}{5}$
Seed 26X.....	$\frac{3}{8}$
Seed 23.....	3
Stanley.....	1

Orthochromatic plates

Cramer's Instant Iso.....	1
Cramer's Medium Iso.....	2
Seed L Ortho.....	$\frac{3}{8}$
Seed C Ortho.....	3
Standard Orthonon.....	1

Panchromatic plates

Cramer's Trichromatic.....	3
Cramer's Spectrum.....	3
Seed Panchromatic.....	3
Wratten M.....	1

Slow plates for special work

Cramer's Contrast (green label).....	6
Seed Process.....	12
Lanternslide, Eastman.....	60
Lanternslide, Imperial Special.....	36
Lanternslide, Seed.....	36
Lanternslide, Standard, blue label.....	18
Lanternslide, Standard, white label.....	18

Plates for color photography

Lumiere's Autochrome with Lumiere's rayfilter.....	72
Hess-Ives Hiblock.....	60
Paget direct colour, with screen and rayfilter.....	24

As in the preparation of the magnification table, so in the preparation of the table of exposure factors for the given magnifications one cannot be guided by the simple rule that exposure stands in direct ratio to the square of magnification. This rule is of great help in preparing the table for a single system, where nothing but the ocular or the extension of the bellows is changed. But when it comes to the use of another objective, two new factors must be taken into account. It is well known that exposure varies as $\frac{1}{(N. A.)^2}$ of the objective, and this formula does not apply to oil-immersion objectives. Moreover, it is desirable to use the optimum position for the substage condenser and this position, as explained in the paragraph on the lighting system is a different one for every objective.

The best way to proceed is, therefore, to ascertain by actual exposure the time of correct exposure for a given magnification for each objective at the optimum position of the substage. Once these are obtained the correct exposures for all other magnifications for each system may be calculated. For example, if you have found that the correct exposure for an Orthonon plate at

100-diameter magnification obtained by the use of an objective apochromate 16 mm. in combination with a projection ocular 2 and optimum position of the substage condenser at mark 5 of your scale is 0.04 second, then the exposure for the same combination at 400-diameter magnification, even if that magnification has been obtained by the use of ocular 4, will be 0.64 second.

Unfortunately, it is by no means easy to decide what is a correct exposure. To ascertain it as nearly as possible it is imperative to use time and temperature development and fractional exposure. My experiments were made with the following developer which has many good qualities, does not stain the fingers or the plate, but must be used fresh in every experiment, since the time of development increases considerably with the use of the developer.

Pyro-acetone developer

Solution A

Water.....	500 cc.
Oxalic acid.....	1 gram
Pyrogalllic acid.....	30 grams

Solution B

Water.....	1000 cc.
Sodium sulphite, dry.....	120 grams

For use take

Water.....	120 cc.
Solution A.....	15 cc.
Solution B.....	30 cc.
Acetone.....	6 cc.

If the mixture has a temperature of about 18.3 to 18.8°C. (65 to 66° F.), then the image of a correctly exposed plate will appear in fifteen seconds and the development will be completed in six minutes from the time the plate was immersed in the developer.

Fractional exposure consists in making four different exposures on the same plate in such a manner that each following exposure is twice as long as the preceding one. These exposures may be represented as a, 2a, 4a, 8a. To make such an exposure, the

slide of the plate-holder must be marked with three parallel lines dividing the plate in four quarters. The slide is opened and the plate is exposed a seconds (or fractions of a second). Now the slide is moved in one quarter and the plate is exposed again a seconds (or fractions of a second). When moved in two quarters the exposure should be $2a$ and when the plate-holder is moved in three quarters the exposure should be $4a$.

The choice of an object to be photographed is also important. A stained section will not do and it is advisable to use a slide which will permit the use of both low- and high-power objectives. I have used the Diatome Arachnodiscus and a thin section of human bone. The time of the appearance of the four images in the developer will at once indicate which exposure is nearest to be the correct one. It is advisable to control the experiment by making another fractional exposure at a higher magnification.

The completed exposure table will consist of as many vertical columns as there are objectives in the outfit, and for each of these columns the optimum position of the substage must be indicated at the top of the columns. A special column on the left of the table will contain all magnifications as accepted in the magnification table.

HOW TO PREPARE A TABLE OF RAYFILTER-PLATE FACTORS

The choice of rayfilters is not entirely a matter of taste. While one can use fluids in special containers, it is simpler and better to buy a set of dry rayfilters from a reliable firm with stated regions of light transmitted. Such filters are more permanent and easier to use. It is not advisable to make dry rayfilters in the laboratory unless the laboratory is provided with instruments which permit the preparation of identical rayfilters at any time in case of inadvertent damage, since a variation in the region or in the intensity of light transmitted would affect the exposure. At the Osborn Zoological Laboratory we have accepted as a standard equipment for all photographic work Cramer's photographic rayfilters. There are ten of them and singly or in combination they transmit the following regions:

1.....	A-6350	3+4.....	6920-5840
2.....	A-6100	3+7.....	5900-5800
3.....	A-5850	3+8.....	A-7000
4.....	A-5400	4+5.....	6870-5525
5.....	A-5250	4+7.....	5900-5660
6.....	A-5100	5+7.....	5900-5400
7.....	5800-5000	5+8.....	5530-5350
8.....	5200-3950	6+7.....	5900-5150
9.....	5200-3500	6+8.....	5350-5150
10.....	Visual luminosity	6+9.....	5600-5200
		7+8.....	5200-5000
		7+9.....	5300-5100

The Wratten 'M' filters transmit somewhat different regions, as shown in their booklet.

If all plates were equally sensitive to the same regions of the spectrum, the same factors would apply for all makes. But experience shows that one brand of plate may be twice as rapid as another in daylight yet be considerably slower with a special rayfilter. Thus the Standard Orthonon is twice as rapid as Cramer's Medium Iso in daylight, and four times as slow in green light in the region 5200-5000. When it comes to the use of red light, nothing but panchromatic plates can be used. The Wratten 'M' plate answers this purpose admirably, but for orange, yellow, and blue light the Orthonon plate is preferable if for no other reason than greater ease and safety in handling it. For green light we use Cramer's Iso Medium or Instantaneous Iso.

To find the correct rayfilter-plate factors it is necessary to use the same slides as were used in the preparation of the table of exposure factors without rayfilter. Fractional exposure with a rayfilter will easily show how much the normal exposure must be prolonged to obtain the same results. A separate exposure experiment must be made for every rayfilter or combinations of rayfilters and plate. Thus was the following table of RP factors obtained, but naturally it is good only for the Cramer rayfilters.

Table of R-P factors for use with Cramer's photomicrographic rayfilters and dry plates. The unit of comparison is the normal exposure for a standard Orthonon plate without rayfilter. The figures are good only when the light is an open arc

CRAMER'S RAYFILTER, SINGLE OR COMBINATION OF TWO	STANDARD ORTHONON PLATE	WRATTEN M PLATE	CRAMER'S MEDIUM ISO PLATE	CRAMER'S INSTANT ISO PLATE
1		250		
2		30		
3	500	15		
4	30		50	
5	15			
6	10			
7	60			
8	15		15	
9	10			
10	5		10	
3+4	600	15		
4+5	30			
4+7	1000			400
5+7	250		100	
5+8	2000		600	250
6+7	100			
6+8	1000			150
7+8	2000		500	250
Without rayfilter	1	1	2	1

THE CHOICE OF THE RAYFILTER COMBINATION

The choice of a rayfilter will naturally depend upon the results to be attained. At times it may be desirable to get as much contrast as possible regardless of the loss of detail, especially if some single structure should be shown clearly. In such cases a rayfilter which makes the structure appear black to the naked eye, i.e., a rayfilter which absorbs all rays transmitted by the structure to be photographed, is the one that will give the best results. If the section has a counterstain, if for example the stain employed was haematoxylin-eosin, and it is desired to show only the structures stained with haematoxylin, then an eosincolored rayfilter which will transmit all rays of that color may be used with advantage. In the majority of cases, however, the photograph will be much more satisfactory, if the contrast is less, but the detail greater. To find the right combination that will answer

this purpose is not an easy matter. One may be helped by an examination of each staining fluid through a direct vision spectroscope, but the final decision has to be derived from an actual exposure. It will be also found that an examination of the image on the screen with different rayfilters will be of great help. In case of doubt, two or three different combinations may be tried and the negatives compared. In the following table is given a list of the commonly employed stains and the best combinations of plate and rayfilter for each.

CORRECT EXPOSURE

The exposure factor multiplied by the R-P factor will give the correct exposure in seconds for the given combination of stain, rayfilter, objective, substage position, and magnification as indicated in the tables. If care is exercised not to overlook a single one of these conditions and to see to it that the source of light is also in its proper place, the only element unaccounted for remains the microscopic slide itself. The quality of the tissue, the intensity of the stain, the thickness of the section, play no inconsiderable part in the determination of the correct exposure. If the tables are prepared from a very thin and transparent section, the deviation in exposure of thick sections will be great. It is therefore advisable in standardizing the apparatus to use either medium thick sections, or else to take the mean of two figures obtained from an exposure of a very thin and a very thick section under identical conditions. No satisfactory rules can be formulated in regard to the transparency factor of the microscopic section, but the student will rapidly learn the necessary increase or reduction in the time of exposure.

As a rule, correct exposure gives the best results. Under circumstances, however, overexposure is desirable and even indispensable. Just as in a brilliantly sunlit room one obtains a much better picture of details if one gives long exposure and develops the plate with a restrainer, so in microphotography details may be brought out by overexposure when some parts of

Table showing the best combination of dry plate and rayfilter for stains in common use, spectral regions transmitted and the R-P factors

STAIN	PLATE	CRAMER'S RAY- FILTER	SPECTRAL REGION	R-P FACTOR
None	Orthonon	None	Entire spectrum	1
None	Orthonon	10	Entire spectrum	5
Acid green+safranin	Instant Iso	4+7	5900-5660	400
	Orthonon			1000
Anilin blue	Orthonon	4	A-5400	30
	Medium Iso			50
Anilin blue+safranin	Orthonon	5	A-5250	15
Azur II	Wratten M	3	A-5850	15
	Orthonon			500
Bielschowsky's silver	Instant Iso	5+8	5530-5350	250
	Orthonon			2000
Bismark brown	Orthonon	8	5200-3950	15
Bleu de lion	Instant Iso	4+7	5900-5660	400
	Orthonon			1000
Carmalum	Instant Iso	5+8	5530-5350	250
	Medium Iso			600
Carmine (all stains, acid, alum, borax, para, picro, etc.)	Instant Iso	5+8	5530-5350	250
	Medium Iso			600
	Orthonon			2000
Erythrosin+cyanin	Orthonon	7	5800-5000	60
Eosin	Instant Iso	6+8	5350-5150	150
	Orthonon			1000
Fuchsin	Instant Iso	6+8	5350-5150	150
	Orthonon			1000
Gentian violet	Wratten M	3	A-5850	15
	Orthonon			500
Gentian violet+safranin	Medium Iso	5+7	5900-5400	100
	Orthonon			250
Giemsa's	Instant Iso	4+7	5900-5660	400
	Orthonon			1000
Gold chloride	Instant Iso	5+8	5530-5350	250
	Medium Iso			600
	Orthonon			2000
Hemalum	Medium Iso	5+7	5900-5400	100
	Orthonon			250
Haematoxylin (all stains Boehmer's, Delafield, Ehrlich, iron, etc.)	Medium Iso	5+7	5900-5400	100
	Orthonon			250

STAIN	PLATE	CRAMER'S RAY- FILTER	SPECTRAL REGION	R-P FACTOR
Haematoxylin+boraxcarmine, con- gored, eosin, erythrosin, orange G, picrocarmine, tetrabromfluor- escic acid	Medium Iso Orthonon	5+7	5900-5400	
Haematoxylin+safranine	Orthonon	5	A-5250	15
Indigo carmine	Wratten M Orthonon	3	A-5850	15 500
Iodine green	Wratten M	1	A-6350	250
Iodine green+acid fuchsin	Instant Iso Orthonon	6+8	5350-5150	150 1000
Methyl green	Wratten M	1	A-6350	250
Methyl green+acid fuchsin	Wratten M	3+4	6920-5840	15
Methyl violet	Wratten M Orthonon	3	A-5850	15 500
Methylen blue+eosin, Romanow- sky, Wasielewski, etc.	Instant Iso Orthonon	4+7	5900-5660	400 1000
Mallory's	Instant Iso Orthonon	4+7	5900-5660	400 1000
Magdala red+anilin blue	Medium Iso Orthonon	5+7	5900-5400	100 250
Nigrosin	Orthonon	5	A-5250	15
Orange C	Orthonon	8	5200-3950	15
Picric acid	Orthonon	8	5200-3950	15
Rose Bengal	Instant Iso Orthonon	6+8	5350-5150	150 1000
Safranin	Instant Iso Medium Iso Orthonon	7+8	5200-5000	250 500 2000
Safranin+acid green, light green	Instant Iso Orthonon	4+7	5900-5660	400 1000
Safranin+gentian violet, picric acid, waterblue	Medium Iso Orthonon	5+7	5900-5400	100 250
Safranin+haematoxylin	Orthonon	5	A-5250	15
Silver impregnation	Instant Iso Orthonon	5+8	5530-5350	250 2000
Sudan III	Instant Iso Orthonon	6+8	5350-5150	150 1000
Tetrabromfluoresceic acid	Instant Iso Orthonon	6+8	5350-5150	150 1000
Toludin blue+erythrosin	Instant Iso Orthonon	4+7	5900-5660	400 1000
Vesuvium	Orthonon	8	5200-3950	15
Victoria blue	Wratten M Orthonon	3	A-5850	15 500

a section are much more transparent than others. In overexposing a plate it is advisable in such cases to know the exact ratio of overexposure as the restrainer should be used in strict conformity with that ratio. The pyro-acetone developer of the formula given above lends itself admirably to such work. I have made a series of experiments in which the correct exposure was first carefully ascertained for a given microscopic slide, and the exposure then increased twice, four times, eight times, sixteen times, thirty-two times, sixty-four times, one hundred twenty-eight, and two hundred fifty-six times. Measured quantities of potassium bromide were added to the developer and fractional exposure used to see the results more clearly. The plates were left six minutes in the developer. A similar series of plates was left seven minutes and a third eight minutes. The best negatives were noted and a fresh plate was exposed same length of time and developed in the same manner as a control. Thus several formulae were obtained, each giving excellent results for the given overexposure. Those who have seen my negative which was overexposed about 130 to 150 times and then developed with the restrainer agree that aside from its yellowish color one would never guess that the plate was overexposed.

a. Pyro-acetone developer for plates overexposed 4 times:

Normal developer	{ Water.....	120 cc.
	{ Solution A.....	15 cc.
	{ Solution B.....	30 cc.
	{ Acetone.....	6 cc.
10 per cent potassium bromide.....		1 cc.
Develop 6 minutes at 65° F.		

b. Pyro-acetone developer for plates overexposed 8 times:

Normal developer as above	
10 per cent potassium bromide.....	2 cc.
Develop 8 minutes at 65° F.	

c. Pyro-acetone developer for plates overexposed 16 times:

Normal developer as above	
10 per cent potassium bromide.....	10 cc.
Develop 8 minutes at 65° F.	

d. Pyro-acetone developer for plates overexposed 32 times:

Normal developer as above

10 per cent potassium bromide..... 20 cc.

Develop 8 minutes at 65°F.

e. Pyro-acetone developer for plates overexposed 130 to 150 times:

Normal developer as above

Potassium bromide (powder)..... 4 grams

Develop 8 minutes at 65°F.

New Haven, Connecticut

April 19, 1920

THEORIES OF CLAVICULAR ORIGIN

Gegenbaur ('64) thought that he had found the human clavicle developing in cartilage, and probably with the anuran shoulder-girdle in mind, claimed that the cartilage present was a remnant of the old precoracoid, thus determining the character of the clavicle as a cartilage bone. It is certainly true that in the frog the precoracoid does enter into and constitute the core of the clavicle, which is overlaid on the anterior side by a membranous element, and it is also true that in many of the mammals the clavicle contains a relatively large amount of cartilage at a fairly early stage. In man the cartilage is of a peculiar kind called by Mall a 'precartilagenous tissue' (figs. 4 to 6).

Gegenbaur has been supported in his view of a precoracoidal contribution to the clavicle by Huntington ('18), and in a private communication to the author concerning the matter Huntington states his position not only on the clavicular complex, but also on the entire shoulder-girdle as follows:

this structure (shoulder-girdle) as a whole represents all the various possible combinations which result from the fact that it develops by the union of two originally distinct and separate elements, the exoskeletal and the primordial cartilaginous girdle, in different degrees in different types.

As regards the clavicle the different proportional amounts of the dermal and cartilaginous contribution is well shown in the different vertebrate classes. The process of envelopment of the precoracoid by the clavicle is developed to a widely varying degree in individual Anure types, up to the complete replacement of the cartilage by an element originally dermal in origin.

In the above statement of Huntington's is a somewhat plausible explanation of the widely different views expressed as to the constitution and homology of the clavicle. Two distinct elements, exoskeletal and cartilaginous, have contributed to it unequally in different classes of vertebrates, and even in different genera of the same class. This is apparently the case in the Amphibia and Reptilia, where the cartilaginous and dermal elements vary from a nearly pure precoracoidal cartilage bone to a purely dermal bone such as that found in many of the reptiles.

The hypothesis of Gegenbaur and Huntington has much to recommend it at first sight and does seem to account for the variations met with in the clavicle of the different groups of vertebrates by the inclusion of a greater or lesser amount of the cartilaginous precoracoid into this element. Assuming that the coracoid process of man is the homologue of the metacoracoid or posterior coracoid of Permian reptiles and the precoracoid to be the cartilaginous part of the clavicle, a most direct and beautiful homology can be drawn between the shoulder-girdle complexes in the frog and man, for which comparison examine figures 1 to 3.

However, as Watson ('17) remarks, the anuran shoulder-girdle is of totally unknown ancestry, and the group as a whole being characterized by extraordinary specialization, any comparisons between the frog and other forms are very hazardous and should receive most careful checking and corroboration. And this is especially true in a comparison with the human shoulder-girdle so long as the homology of the coracoid process is still in doubt. Further on I shall attempt to show that the coracoid process is the homologue of the precoracoid rather than the metacoracoid, and, if this be true, the theory of Gegenbaur and Huntington is no longer tenable.

Broom ('99) was the first to cast doubt upon Gegenbaur's hypothesis. He claimed that, while cartilage was present in the clavicle, it did not appear until after ossification had begun in the dense connective tissue, and concluded therefore that the clavicle was a purely membrane bone. Broom examined a number of marsupials, reptiles, and other Tetrapoda, including man, and found that in all these ossification of the clavicle preceded the appearance of true cartilage cells.

Mall ('06) studied by the Schultze method of clearing, the ossification centers in an extensive series of human embryos less than 100 days old. He was the first to announce the dual origin of the clavicle from two distinct centers of ossification, a medial and a lateral. Mall did not, however, give an opinion on the significance of these two centers.

Fawcett ('13) examined a series of human embryos sectioned transversely and otherwise, and found in serial sections the two

centers of ossification Mall had seen in cleared specimens. Ossification began in the outer end of the inner half of the clavicle and in the inner end of the outer or acromial part of the clavicle. No cartilage cells were present until after the appearance of these two ossified centers. At this stage the inner and outer parts of the clavicle had no connection, but were separated by the investing perichondrium. In the 19-mm. stage (crown-rump measurement) a bony bridge develops and connects the two centers (figs. 6 to 9).

Another important point made by Fawcett is that the connection of the coracoid-clavicular ligament is always with the acromial half of the clavicle, and not, as Fitzwilliams ('10) thought, with its sternal end. In cases of cranio-cleido-dysostosis Fitzwilliams found a ligament connecting the inner part of the clavicle with the base of the coracoid process. He identified this as the coracoid-clavicular ligament and urged that it was in cases of this disease a prolongation of the coracoidal contribution to the sternal part of the clavicle. That Fitzwilliams is incorrect in his identification of this ligament is beyond all doubt, as is shown very clearly in figures 6 and 7. In all the specimens I have examined in the Mall Collection, the coracoid-clavicular ligament extends from the acromial half of the clavicle to the coracoid process, and Fawcett found the same thing in his material. Watson ('17) publishes a photomicrograph of a cross-section through the shoulder region of the marsupial *Trichosurus*, which shows that in this group also, as in the primates, the coracoid-clavicular ligament is attached to the acromial part of the clavicle.

It is admitted by all investigators that at a comparatively early stage cartilage does appear in the clavicle in considerable quantity and contributes to the ossification process. The question seems to hinge on the amount and character of the cartilage present and whether this has morphological significance such as is attributed to it by Gegenbaur, Huntington, Fitzwilliams, and Paterson or is merely a neomorph comparable to the cartilage in the mandible and other membrane bones (Broom, Fawcett, Watson).

Paterson has a number of papers on the shoulder-girdle and has briefly stated his views on the homology of the clavicle in his 1902 paper as follows: that the clavicle possibly contains more than one morphological unit (judged by its ossification, directly in the outer part, indirectly through cartilage in the inner part).

Fitzwilliams ('10) also maintains that there are two distinct elements involved in the origin of the clavicle, one is a dermal element and is confined to the outer half of the clavicle, while the other is cartilaginous and represents the precoracoid of the lower forms. His arguments for the dual origin of the clavicle are the most complete and strongest on that side of the question. They may be summed up as follows:

a. There are two centers of ossification present in the clavicle, and this may well indicate that the bone is a composite one and may be traced back to dissimilar elements in lower forms.

b. It is pointed out that the inner end of the element is a round bone, and here is found the greater amount of the cartilage present. Round bones are, in general, cartilage bones, and this argues in favor of the inner half of the clavicle being of cartilage origin. On the other hand, the outer half is flattened and has more the characteristics of the flat bones of the skull which are membrane bones. The first center of ossification also appears in the outer half and is well advanced before cartilage appears.

c. The disease known as cranio-cleido-dysostosis attacks membrane bones principally, and when present in the clavicle the outer part is usually the one affected, while the inner half remains normal. This again points to the inference that the outer half of the clavicle is of membranous origin, the inner half cartilaginous.

d. There is, after all, a rather large deposit of cartilage present in the developing clavicle, and as this cartilage enters into and becomes a part of the bony product, it may have had an ancestral history.

e. The above points are emphasized by the known conditions in the Anura, where the precoracoid becomes the cartilaginous core of the investing dermal tissue, the two elements quite clearly uniting to form the anuran clavicle.

f. The clavicle, therefore, according to this point of view, is the result of two interacting tissues, one a dermal element and the other cartilage, which contribute unequally in the different classes of vertebrates to this structure, so that investigators finding one or the other elements greatly in excess in the form immediately under observation were led to take such divergent views as above indicated.

The three theories of clavicular origin now in the literature are set forth with their respective sponsors in the following table:

	CARTILAGINOUS CLAVICLE	DERMAL CLAVICLE	MIXED CARTILAGINOUS AND DERMAL CLAVICLE
Broom ('99).....		*	
Fawcett ('13).....		*	
Fitzwilliams ('10).....			*
Gegenbaur ('64).....	*		
Gotte ('77).....	*		
Hoffman ('79).....	*		
Huntington ('18).....			*
Paterson ('02).....			*
Watson ('17).....		*	

OBSERVATIONS

Recently I have had the privilege of examining the cleared specimens of human embryos upon which Mall ('06) based his paper on ossification centers, and also have studied the earliest stages of the clavicle in the splendid collection of serial sections of human embryos in the Carnegie Laboratory of Embryology at the Johns Hopkins Medical School.¹ My purpose was to determine, if possible, between the view of Broom and Fawcett that the human clavicle is a pure membrane bone, and that of other investigators who see in the clavicle a persisting remnant of the old precoracoid.

¹ It is my pleasure to acknowledge the courtesy extended me by Dr. George L. Streeter, of the Carnegie Laboratory of Embryology, in placing the facilities of the laboratory and the series of human embryos in his charge at my disposal during the summer of 1919.

So far as I am aware, there was no prejudicial bent of mind toward either theory, and I am not committed to either side of the controversy by any statement in my published papers on shoulder-girdle problems.

The result of my examination of all the evidence available may be summed up briefly as follows:

A. The material at my command, the Mall Collection, than which there is no better or larger collection of human embryos anywhere to be found, confirmed in all essential particulars the observations of Broom and Fawcett. Ossification begins approximately about the thirty-ninth day and is by two distinct centers, one in the lateral half and one in the medial half of the clavicle. At this time the bony centers are surrounded by the 'peculiar precartilaginous tissue,' which certainly is not hyaline cartilage. It seems quite clear that *the earliest stage of ossification in the clavicle, both in its medial and lateral halves, is a dermal ossification*, and that cartilage is entirely lacking at the time of the appearance of the two centers of bony tissue. This one fact was sufficient to justify Broom and Fawcett in excluding the pre-coracoid as a morphological element of the human clavicle (figs. 10 to 13).

B. In addition to the confirmation above, my special contribution to the subject consists in an attempt to show that the pre-coracoid has a history so different from that contemplated by those who see in the cartilage the old pre-coracoid, that this cartilage could not possibly be that element. I have traced the history and homologies of the pre-coracoid recently (Hanson, *Anat. Rec.*, vol. 19), and the conclusions therein set forth may be recapitulated briefly here.

1. It has been shown by Broom for Australian marsupials, and the author for the American opossum, that in the embryo and fetus of these forms the shoulder-girdle consists of a scapula, clavicle, and two coracoid elements, one of which, the posterior (fig. 2), extends from the scapula to the sternum and is comparable directly with the coracoid of the monotremes. The anterior element of the marsupial fetus is a broad fan-shaped sheet of mesenchyme, of short duration in embryonic life, and is the homologue of the epicoracoid of monotremes.

2. Development shows that the posterior of the two coracoid elements of the fetal marsupial girdle becomes the small rudimentary coracoid process attached to the scapula in the adult, which process undoubtedly is homologous with the same-named process in man. This gives a clear line of genetic relationship from the coracoid process of man to the posterior element in the girdle of the monotremes.

3. Gregory and Camp ('18) and the author have shown that the conditions in the monotreme girdle are so clearly reptilian in character and approximate so closely in every respect to the structure of the girdles in *Sphenodon* and lizards that genetic relationship and homology exist between them.

4. Williston ('11) has practically demonstrated that the coracoid of living reptiles is derived from the anterior bony coracoid element (precoracoid) of Permian reptiles.

5. Therefore, if the coracoid process of man is the same element as the posterior coracoid of monotremes, and this latter is directly comparable with the posterior of the two coracoids of *Sphenodon* and lizards, which is in turn a derivative of the precoracoid of Permian reptiles, then the coracoid process of man equals the anterior bony element of Permians, and *the precoracoid is the true coracoid*.

6. It seems to be pretty well established that the coracoid process of placentals is a precoracoid, so that this bone is fully accounted for without reference to the clavicle. It might be suggested that the part of the precoracoid which has aborted is the piece found in the clavicle, but it has been shown clearly by Broom that the clavicle is fully formed and contains its maximum amount of cartilage long before the degeneration of the precoracoid, i.e., the fully formed precoracoid extending from scapula to sternum (fig. 2) persists for a considerable time after the ossification of the clavicle has begun and the cartilage at its ends is present. The two, fully formed clavicle and precoracoid, are in marsupials coexistent and separated by a considerable space. There is, therefore, no way for the cartilage of the precoracoid to enter the clavicle in mammals.

CONCLUSION

The fact that the cells in the early clavicle are clearly not hyaline cartilage cells, but a peculiar tissue of which little seems to be known, coupled with the demonstration by the author that the well-developed clavicle and complete precoracoid extending from the scapula to the sternum are coexistent in the embryo, and the stages of the degeneration of the precoracoid having been followed completely in marsupials by Broom, excluding the possibility of the entry of precoracoidal tissue into the clavicle, apparently indicates that there are pretty solid grounds for considering the human clavicle to be a purely dermal bone.

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PLATE 1

EXPLANATION OF FIGURES

1 Shoulder-girdle and lateral half of sternum and epicoracoidal cartilages of the bull frog. The precoracoid becomes the cartilaginous basis of the clavicle. In this form the clavicle is derived from two sources, the precoracoid and the dermal ossification.

2 Reconstruction of the shoulder-girdle of a marsupial fetus. Note that the coracoid reaches to the sternum. This is the same coracoid that a little later in development aborts, the only remains of which is the rudimentary coracoid process attached to the anterior side of the neck of the scapula. The complete coracoid is present, however, long after the clavicle is fully ossified, and if this element (coracoid) is the precoracoid, as I hold, there is no possibility of its contributing to the cartilage of the clavicle. After Broom.

3 Schematic diagram of shoulder-girdle of man. Compares pretty closely with figure 1 of the anuran shoulder-girdle. However, the resemblance is superficial only (see text) and not genetic. After Huntington.

ABBREVIATIONS

<i>Ac</i> , acromian	<i>Oss</i> , os suprasternalia
<i>CC</i> , costocoracoid ligament	<i>Ost</i> , omosternum
<i>Cl</i> , clavicle	<i>PCr</i> , precoracoid
<i>Cr</i> , coracoid	<i>R¹</i> , first rib
<i>ECr</i> , epicoracoid	<i>Sc</i> , scapula
<i>Ep</i> , sternal epiphysis of clavicle	<i>SSc</i> , suprascapula
<i>Hu</i> , humerus	<i>St</i> , sternum
<i>Ic</i> , interclavicular ligament	

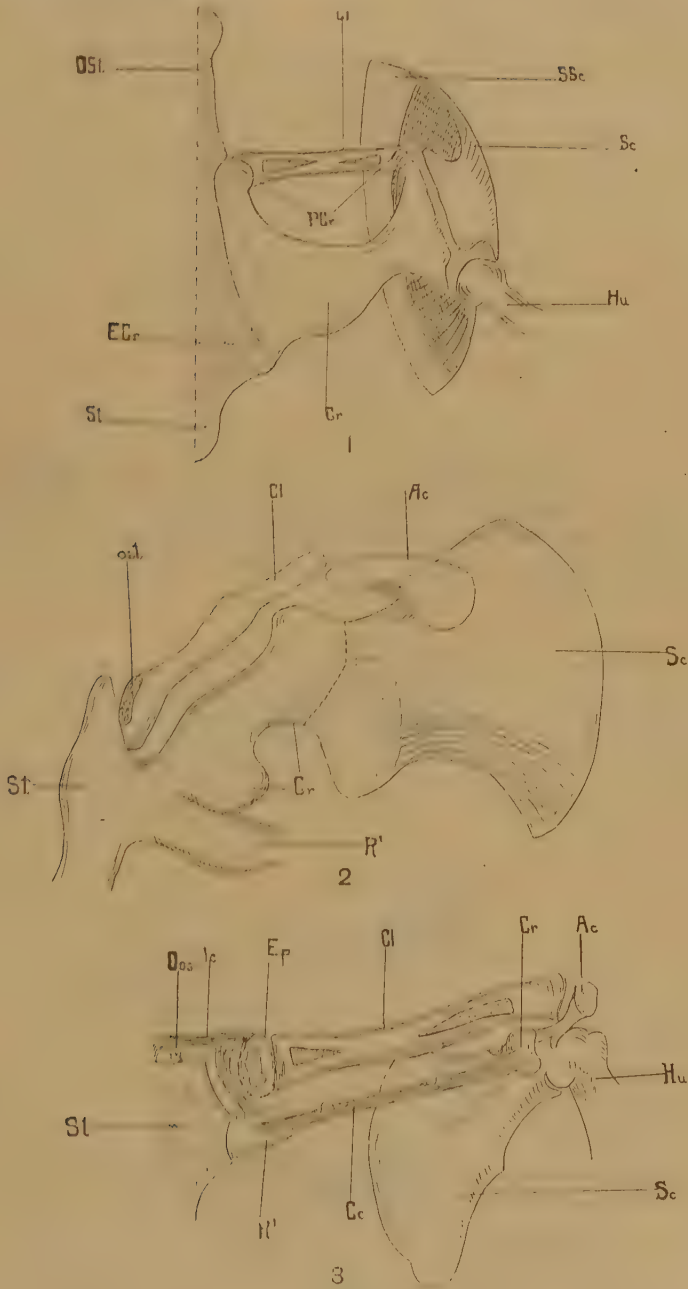


PLATE 2

EXPLANATION OF FIGURES

4 to 9 A series of stages showing the ossification of the clavicle from two distinct centers. Note that the coracoid-clavicular ligament is attached to the acromial half of the clavicle. This series of figures is modified after Fawcett and checked in all particulars by a careful examination of a large series of human embryos.

ABBREVIATIONS

<i>B</i> , ossification center	<i>C Cl Lig</i> , coracoid clavicular ligament
<i>Br</i> , bridge of connective tissue between two parts of clavicle	<i>CT</i> , connective tissue
<i>C</i> , cartilage	<i>DT</i> , deltoid tubercle
<i>CC</i> , young cartilage cells	<i>O</i> , bony bridge, connects two centers
	<i>PC</i> , precartilaginous tissue

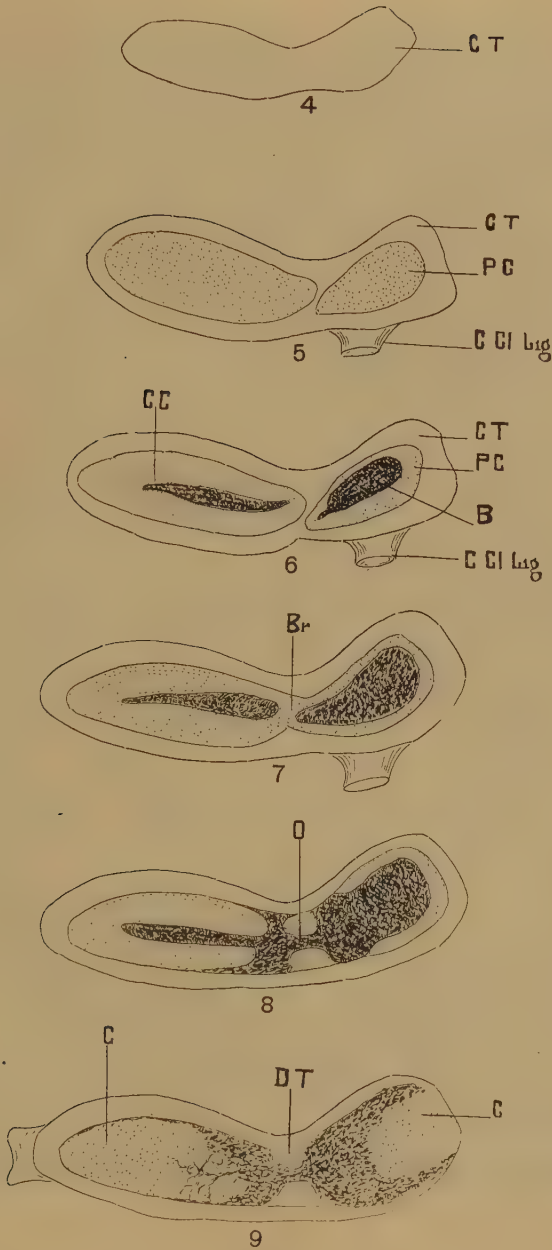


PLATE 3

EXPLANATION OF FIGURES

10 Photomicrograph of developing clavicle, showing two centers of ossification. This and the following three photomicrographs are introduced to show several stages of the developing clavicle as it actually appears under the microscope. Together with a large number of others, they constitute the basis for the schematic figures 4 to 9 and the conclusions reached in this paper. Series 240, slide 26, section 1. $\times 29$. Mall Collection, Carnegie Laboratory of Embryology.

11 Older stage than above. Outer half of clavicle fully ossified, inner half lags in ossification process and more cartilage is present in this part. Ossification is ectochondrial. Series 460, slide 19, section 7. $\times 29$. Mall Collection, Carnegie Laboratory of Embryology.

Cl, clavicle

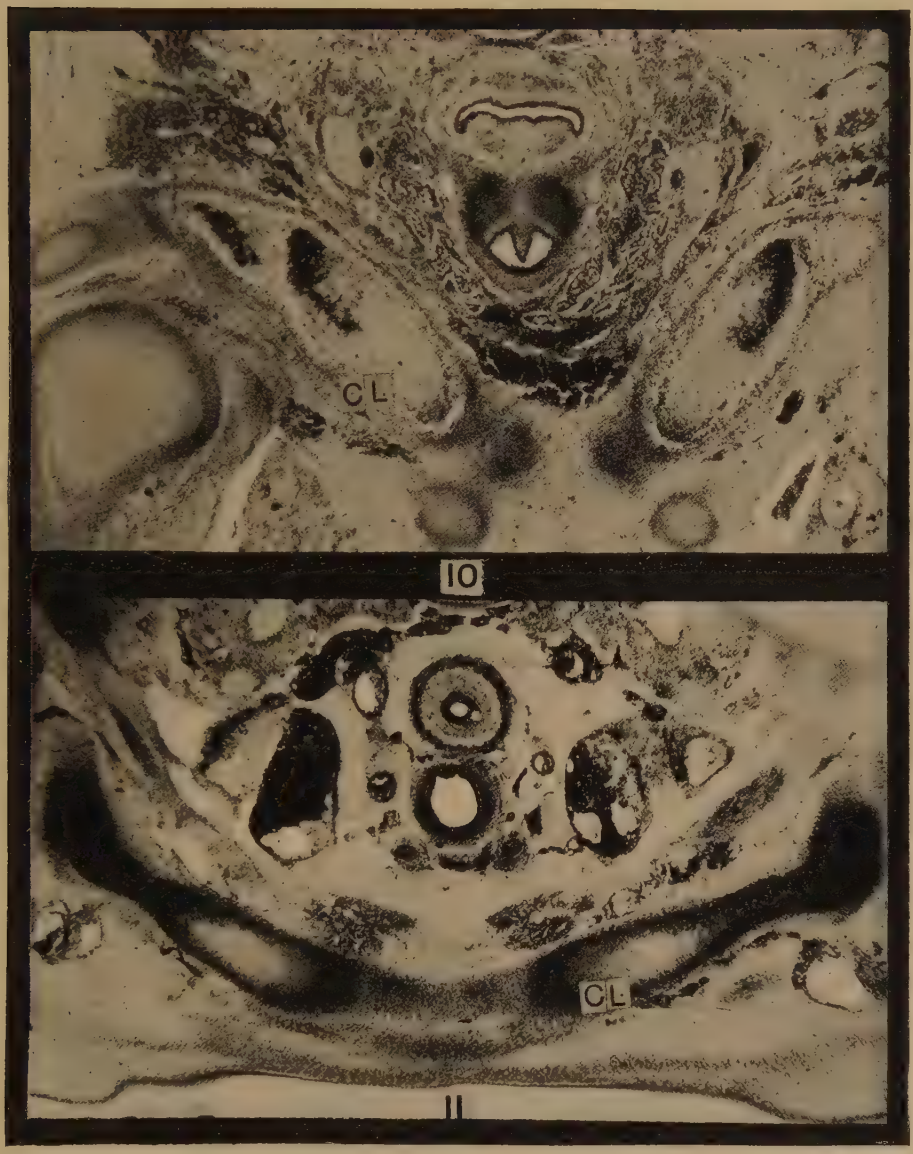


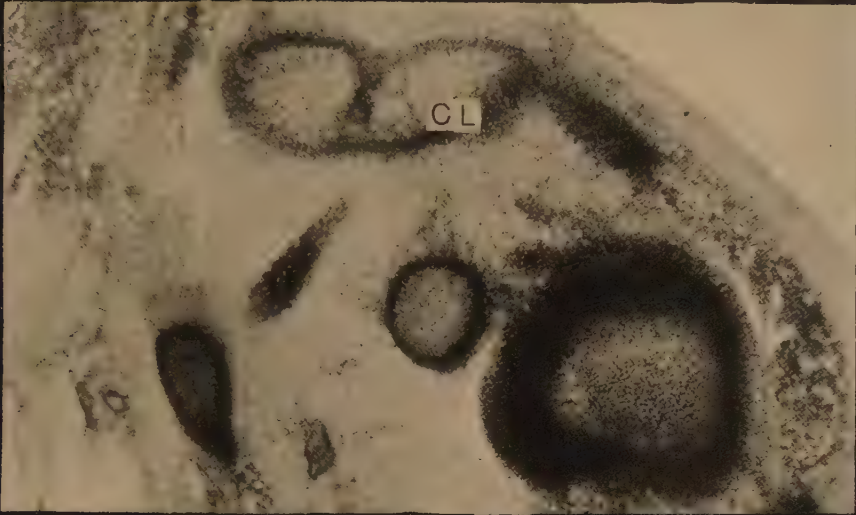
PLATE 4

EXPLANATION OF FIGURES

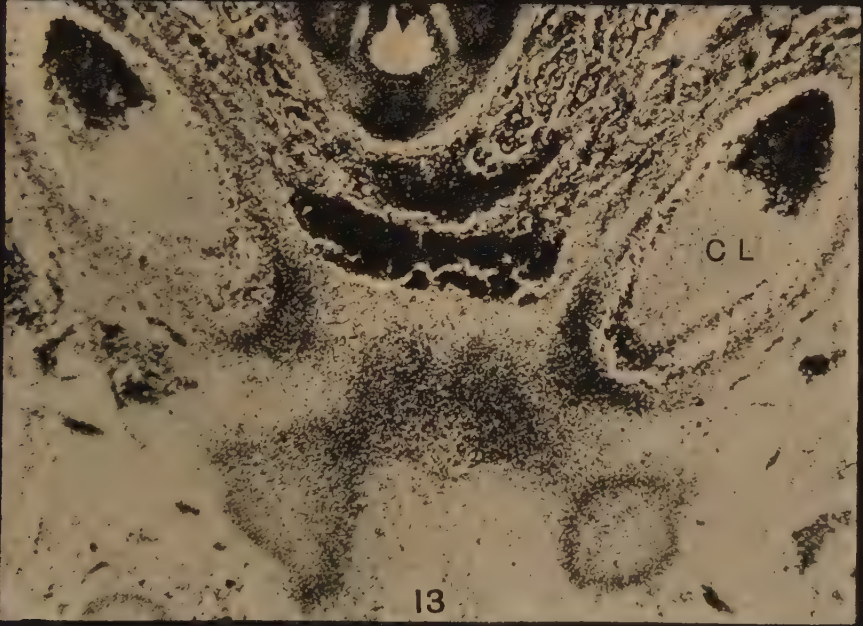
12 The two parts of the clavicle are beginning to fuse, Series 1324, slide 26, section 6. $\times 55$. Mall Collection, Carnegie Laboratory of Embryology.

13 Photomicrograph of developing clavicle, showing acromial center of ossification well established and inner center just beginning around the lower outside edge of clavicle, an ectochondrial ossification. Series 240, slide 26, section 8. $\times 48$. Mall Collection, Carnegie Laboratory of Embryology.

Cl, clavicle



12



13

Resumen por el autor, Frank Blair Hanson.
Universidad Washington, Saint Louis.

El problema del coracoides.

El embrión del opossum americano, *Didelphys virginiana* posee un coracoides, que, lo mismo que en los monotremas, se extiende hasta el esternón, uniéndose con él en un punto situado entre la clavícula y la primera costilla. Esta última se atrofia y deja un pequeño proceso rudimentario, conocido en el adulto con el nombre de proceso coracoideo.

A la parte descriptiva sigue una discusión de la homología del proceso coracoideo del hombre, esforzándose el autor en demostrar que el proceso coracoideo del hombre es el homólogo del precoracoides de los reptiles fósiles del Pérmico.

Translation by José F. Nonidez
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THE PROBLEM OF THE CORACOID

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TWO PLATES (SEVEN FIGURES)

INTRODUCTION

The phylogeny of the coracoid presents one of the most fascinating and elusive problems of vertebrate morphology. The literature is extensive. The number of conflicting theories and the confusion of the nomenclature is hardly paralleled in the history of any other vertebrate structure. This is due, in part, to its long history, occurring as it does in the Elasmobranchii and found in every group of animals from the dogfish up to man; also, in part, to the radical character of the modifications undergone in the different groups through adaptations to structural and functional demands. A long history of structural changes in a region of progressive functional differentiation, and, complicated further by the presence of both dermal and cartilage bones, gives an ideal situation for exactly what has happened in regard to our knowledge of the coracoid.

One is at times disposed to pigeon-hole this problem among the insolubles, or at least await patiently and in silence for the somewhat remote possibility of turning up some new evidence from paleontological specimens yet to be collected.

However, this is one of those haunting problems that refuses to be pigeon-holed, and, once infected by its appeal, the investigator finds himself returning to it again and again.

DIFFICULTIES OF THE NOMENCLATURE

As indicated above, the nomenclature of the coracoidal elements of the different groups is terribly involved and confusing. Different authors apply the same name to very different structures, and again different names to the same structure.

In reading the literature on the subject it is necessary, first of all, to ascertain just which element each author has in mind when using the terms metacoracoid, coracoid, epicoracoid, precoracoid, procoracoid, and subcoracoid. As an example of this, Cuvier in 1826 applied the term 'epicoracoid' to the anterior coracoidal element in monotremes. W. K. Parker and others use this same term in speaking of the cartilaginous element on the ventral ends of the coracoids in the frog, alligator, etc., while by Case, Williston and Gregory this same term is used to designate the unossified element found in some fossil reptiles anterior to the two ossified coracoids. A few remarks may clear up the matter somewhat.

In the first place, the term 'epicoracoid' was first given to the anterior element in the monotremes, and by priority should be retained in this connection. The ventral median cartilages of the coracoids of the frog, alligator, etc., have no claim to this name except through the usage of Parker ('67). These cartilages might better have the term 'infracoracoid' applied to them, which would be a suitable and descriptive term and would pair well with the corresponding dorsal cartilage, the suprascapula.

Second, the term 'subcoracoid' may now be discarded. It was formerly applied to the small element on the anterior side of the glenoid fossa in man, and, as its name indicates, was thought to be a vestigial coracoid element. There is now general agreement (*infra*) that this small bone is a neomorph and not of phylogenetic interest. This disposes of one term from the list.

Third, the terms 'precursoracoid' and 'procoracoid' are synonymous, some authors preferring one and some the other, while a few use them interchangeably. By pre- or pro-coracoid is understood the anterior of the two ossified elements of Permian reptiles, but not the most anterior of all, which is a cartilaginous epicoracoid (*infra*).

Fourth, 'metacoracoid' is the name given by Williston to the most posterior coracoid of the Permian reptiles.

Fifth, the simple term 'coracoid' has been so long applied to the coracoid process of man, that it must be retained in this service and its ancestry sought either in the metacoracoid or precoracoid of Permian fossils.

If Broom and Watson are correct in their contention that the metacoracoid of Permians is the homologue of the coracoid process of man, then the metacoracoid is the true coracoid. On the other hand, if the arguments set forth in this paper are valid, the precoracoid is the true coracoid of man.

An examination of the shoulder-girdle of *Moschops* (fig. 5) will give the correct names of these coracoid elements and their relations to one another when all are present.

THE MARSUPIAL CORACOID

Broom ('97, '98, '99, '02, '12), in a series of papers on the shoulder-girdle of the Australian marsupials, has demonstrated that in all the genera studied by him the coracoid extends to and connects with the sternum during early developmental stages.

This embryonic coracoid extends from the anterior part of the glenoid cavity to a position on the sternum between the clavicle and first costal cartilage. In the earliest stages there are no sutures between these parts (scapula, coracoid, sternum), but the whole is one continuous mesenchymatous and later precartilaginous mass.

The adult marsupial has only a small rudimentary coracoid process (fig. 7) attached to the scapula, not relatively larger than in the higher mammals and man. The transition between the condition in the embryo and that in the adult form is, according to Broom, by a process of degeneration, beginning near the middle portion of the fetal coracoid. This progresses in each direction, completely destroying the sternal half, but only incompletely destroying the scapular half, leaving the well-known rudimentary coracoid process of the adult attached to the anterior side of the neck of the scapula.

This embryonic coracoid of the marsupial has on its anterior border a 'fan-shaped cellular element' which does not participate in the glenoid and is of even shorter duration than the posterior element. Broom considers this anterior element to be an epicoracoid and homologous to the element in the monotremes known by this name and having precisely the same shape, position, and relations.

The posterior fetal coracoid of the marsupial has exactly the same position and relations to the scapula, clavicle, and sternum as has the posterior coracoid in monotremes, and the two are quite certainly homologous.

It appears from this work of Broom that *the embryonic shoulder-girdle of the Australian marsupial is identical with the adult girdle of the monotreme*. I state this strongly at the outset because of the bearing it seems to have upon the whole question of the homology of these elements. In this identity is wrapped up one of the clues to the homology of the coracoid process of man.

Formerly it was impossible to pass from the reptilian-like girdle of the monotremes, with its coracoid complete from scapula to sternum, up to the girdle of the adult marsupial, and higher mammals, with a mere rudimentary process attached to the scapula. The development of the marsupial, however, demonstrates in the clearest manner how the coracoid process of the adult passes through a monotreme-like stage with a coracoid extending from sternum to scapula, and how by absorption and degeneration all is lost except the small process on the adult scapula.

Since the work of Broom has an important bearing upon the solution of the long-vexed question of the phylogeny of the coracoid process of man, the question may arise whether his observations and interpretations are correct. Watson ('17), a very careful worker, has verified Broom's results in at least one species of marsupial, *Trichosurus*. Watson made reconstructions in wax of the parts under discussion and showed that conditions were exactly as described by Broom.

Recently I have had the opportunity¹ to examine several series of transverse and frontal sections of *Didelphys virginiana*, the American opossum, and have found that in our native marsupial as in his Australian relatives the coracoid is a solid bar of mesenchyme and later of young cartilage cells, extending without sutures from the scapula to a point on the sternum between the clavicle and first rib (figs. 1 and 2).

¹ My appreciation is hereby expressed to Dr. J. L. Bremer, of the Department of Anatomy of the Harvard Medical School, for the privilege of examining the marsupial slides in the Harvard Embryological Collection.

In older stages the coracoid has parted company with the sternum, and that process of absorption, described by Broom for the species studied by him, has begun, which will eventually leave it in the adult but a mere finger-like projection on the anterior neck of the glenoid (fig. 7).

Since the shoulder-girdle of the American opossum was found to be in all essential aspects the exact counterpart of the anterior girdle in its cousins of Australia, no detailed description is necessary here, and I may proceed at once to the discussion of the homology of the coracoid process of man.

THE HOMOLOGY OF THE CORACOID

Broom ('99) in describing the shoulder-girdle of a 17-mm. mammary fetus of the marsupial *Trichosurus*, says of the coracoid that it is of "much the same absolute size as in the 14.8 mm. stage, and is thus considerably smaller relatively." Broom's work on many species of marsupials shows that as development proceeds the coracoid which once reached the sternum in the embryo and fetus is in the adult only a small process attached to the scapula.

I have observed much this same thing in higher mammals where the coracoid process is relatively much larger in the embryonic stages than in the older fetal stages. Even in the pig, which in the adult has no coracoid process, a small coracoid is present in the embryo and diminishes in size with development. This is also strikingly true in the mouse and human embryos.

Broom has demonstrated conclusively that the coracoid process of adult marsupials is a persisting rudiment of the coracoid which in the fetus extends from the scapula to the sternum. The coracoid of marsupials, therefore, is homologized definitely with the coracoid process of higher mammals and man on the one hand, and with the posterior of the two coracoid elements in the monotremes, for in all their morphological relations the two coracoidal elements of the fetal marsupial can be compared directly with the two coracoids of the monotreme. Thus the homologies of the mammalian coracoid may be stated as follows: the anterior and posterior elements of the monotreme girdle are the epicoracoid and coracoid, respectively; and these are the

homologues of the two similar elements found by Broom in Australian marsupials; and the author in the American species.

The anterior of these two elements (epicoracoid) in the monotremes is a permanent feature of the adult skeleton, but disappears in the adult marsupial and does not reappear in higher forms. The posterior element, the coracoid, is a stout element in the monotremes and is present in the adult as in the fetus, while its marsupial homologue is the exact counterpart in the fetal condition, this later gives way through degeneration to the relatively small element (fig. 7) attached to the scapula in the adult. The coracoid process of mammals is, therefore, the homologue of the strong posterior coracoidal bar which connects with the sternum in the monotremes. That this is the correct view of the coracoid homologies between monotremes and marsupials and higher orders of mammals probably will not be seriously questioned.

In passing from the monotremes to the reptiles there is a variety of opinion which is quite revealing of how little after all we have grasped of the real phylogeny of the mammals.

Broom derives the present-day reptiles from a line of Permian ancestors in which the posterior coracoid was gradually lost, leaving the coracoid of *Sphenodon*, lizards, and the single coracoid of the alligator as the homologue of the anterior coracoid element of the Permians. He, then, derives the mammals from another line of Permian stock in which just the reverse process occurred, i.e., the anterior element now is thought to be the one lost and the posterior retained and homologous with the posterior element of monotremes and the coracoid process of other mammals.

Williston ('11) admits the possibility, and even the probability, of two divergent lines of evolution, one in which the posterior coracoid is lost and leading to present-day reptiles, and one in which the anterior coracoid is lost, leading to the mammals, and he also points out that the absence of the coracoid foramen in the mammals may indicate that this has been the case. However, Williston is very positive that the coracoid of *Lacertilia*, *Dinosauria*, *Crocodilia*, etc., is absolutely identical with the cora-

coid of *Seymouria* and *Varanosaurus*, which is without doubt the anterior coracoid. He says:

there cannot be the least doubt but that the posterior bone, the so-called coracoid, is unossified in *Seymouria*, as in *Varanosaurus*. . . . The coracoid of all these forms consists exclusively of the anterior element, the so-called procoracoid. That this bone has entirely disappeared in all later reptiles, giving place in its entirety to another bone, here unossified, with like attachments, and with its perforating supracoracoid foramen in the same position, I cannot believe. It seems to me utterly improbable that the coracoid as ossified in the *Seymouria* and *Varanosaurus* is not identical with the bone supposed to be (without proof) the fused coracoid and procoracoid of *Lacertilia*, *Dinosauria*, etc., the only thing I wish to insist upon is that the coracoid of *Seymouria* and *Varanosaurus* is absolutely identical with the coracoid of the *Lacertilia*, *Dinosauria*, *Crocodylia*, etc.

Again discussing this same point under the genus *Varanosaurus*, Williston says:

the absence of a posterior bone in this genus, as in *Seymouria* is remarkable. The whole pectoral girdle of *Varanosaurus* has an almost absolute superficial identity with that of the lizards. Under the usual interpretation, however, the large ossified coracoid of *Varanosaurus*, with its close resemblance to the coracoid of *Varanus*, for instance, in its supracoracoid foramen and fenestra, is the metacoracoid. In other words it is assumed that the coracoid of *Varanosaurus* has disappeared gradually by the encroachment upon it of the posterior bone, the so-called true coracoid, which here in this genus was so degenerate that it no longer was even ossified. It seems to me that the utter absence of any proof that such has been the course of evolution in the pectoral girdle of reptiles—for no intermediate form has ever been discovered, no form in which the posterior bone has even reached as far forward as the supracoracoid foramen—is sufficient to throw great doubt upon the hypothesis, a doubt that becomes quite conclusive in the proof afforded by the various specimens of these and other Permian reptiles.

It is a curious fact also that a posterior coracoid bone has never been observed in any temnospondyl, though the sutural division between the scapula and coracoid I have observed in specimens referred to *Aspidosaurus* to be quite as in *Seymouria*.

Williston's work is quite conclusive in homologizing the coracoid of *Sphenodon*, lizards, and crocodiles with that of the anterior element (precoracoid) of Permian reptiles.

Is it possible to pass from the lizards and *Sphenodon* to the monotremes? is the question now facing us. For if we accept the above arguments on the homology of the posterior element of monotremes with the coracoid process of mammals, and also assent to Williston's view that the single coracoid of lizards and *Sphenodon* is the homologue of the precoracoid of fossil reptiles, then by bridging the gap between monotremes and living reptiles we shall have completed the homology of the coracoid from early Permian reptiles up to man.

Gregory and Camp ('18) have compiled the evidence or given the basis for this latter homology between monotremes and living reptiles. In the first place, it has been shown that the single coracoid of *Sphenodon* "gives origin on its ventral surface to a group of muscles comprising the biceps and the three branches of the Coracobrachialis, which group appears to be precisely homologous with a similar group of muscles carried by the ventral surface of the coracoid of monotremes." The subcoracohumeralis of *Sphenodon* arises on the dorsal surface of the coracoid and is homologous with the similarly placed muscle, subcoracoideus, of the monotreme. As far as evidence from muscle goes, the coracoid (= precoracoid) of *Sphenodon* is identical with the coracoid of monotremes. Secondly, the epicoracoid of *Sphenodon* and the lizards is widely excluded from the glenoid exactly as in the monotremes and the embryos of marsupials. The relations of the epicoracoid to coracoid, clavicle, and interclavicle are also identical in monotremes and living reptiles, and in each the ventral surface of the epicoracoid carries the anterior part of the supracoracoid muscle. Comparison of the monotreme coracoid with that of the alligator shows practically the same thing. While there is only one coracoidal element (= precoracoid) in the alligator, Gregory thinks that with the loss of the clavicle in this form there undoubtedly also was lost a membranous epicoracoid which lay between the interclavicle and the coracoid. If this should prove to be the case, the identity between the monotreme girdle and that of the Crocodilia is quite complete.

In general, to quote again from Gregory and Camp ('18), "the whole complex of relations of the epicoracoid and coracoid

of monotremes to each other and to the scapula, clavicle, and interclavicle, is practically identical with the relations of the same set of elements in lizards and *Sphenodon*" (figs. 3, 4, 5, and 6).

There is, then, considerable evidence for comparing directly the coracoid of monotremes with that of living reptiles, and, as shown above, Williston, Broom, Gregory, and Watson unite in homologizing the single coracoid of crocodiles and *Sphenodon* and the posterior element in lizards with the precoracoid of Permian reptiles.

If this reasoning is valid, then the coracoid process of man is a precoracoid and the homologue of the single coracoid of such Permians as *Seymouria* and *Varanosaurus*, and likewise homologous to the anterior element of those Permians which possess two bony coracoids.

Another question yet remains to be disposed of. If the coracoidal elements of the monotremes, *Sphenodon*, and the lizards are the homologues of the anterior element of Permian reptiles, what is the phylogeny of the so-called anterior element or epicoracoid of living reptiles and monotremes? Only one explanation has been offered, and that by Gregory and Camp, to the effect that in such a Permian as *Moschops* (fig. 5) and probably in others, there was really an epicoracoidal cartilage present between the precoracoid and the clavicle and interclavicle. At least in fitting the bones of the shoulder-girdle of *Moschops* together, it was found that there was a space between the clavicles, interclavicle, and precoracoids which must have been filled by the epicoracoids as in *Sphenodon*, lizards, and monotremes. The same thing is indicated in *Eryops*. As shown above, the epicoracoid, often appearing transiently as an embryonic structure in the marsupial, disappears from all higher forms.

This means, of course, that according to Gregory there were originally three coracoid elements—metacoracoid, precoracoid, and epicoracoid—rather than the two usually considered. The admission of a third coracoid (epicoracoid) is denied by Watson, who says (in a private letter) "that the presence of a distinct ossified 'epicoracoid' (as a third anterior element) in Permian vertebrates has never been proven."

While the existence of a third epicoracoidal element has not been proved by the demonstration of an actual specimen from Permian strata, there are several strong indications that such might have been the case. One of these has already been mentioned, namely, that in the Permian Moschops between the precoracoid, clavicle, and interclavicle, there is a space directly comparable with the one filled by an epicoracoid in the lizards and Sphenodon. Since the epicoracoid is a broad thin plate of membranous tissue, it naturally would be lost in the process of fossilization. Other evidence that the epicoracoid was a fairly constant element of Permian reptiles is furnished by Case ('07, '11 a, '11 b). Describing the skeleton of *Dimetrodon dollovi*anus, he says, "the procoracoid terminates anteriorly in a thin, straight edge, which shows signs of having borne a heavy epicoracoidal cartilage." *Dimetrodon* has an ossified coracoid and a precoracoid, and if Case is correct, it also carried a heavy cartilaginous epicoracoid on the anterior edge of the precoracoid. Since the cartilage would not be preserved, we have probably as near a demonstration of the presence of three coracoidal elements (metacoracoid, precoracoid, and epicoracoid) in Permians as will ever be obtained. That this is not an isolated case is shown in two other illustrations taken from Case.

Describing the genus *Diadectes* Cope, Case ('11 a) says of the shoulder-girdle, "the coracoid and precoracoid are not separated from the scapula by suture. . . . The anterior edge (of the precoracoid) is nearly straight and shows the attachment of a *cartilaginous epicoracoid* of considerable size." And again, Case ('11 b), quoting Cope's description of *Eryops megacephalus*, gives the following account of the girdle: the coracoid is but little incurved; its internal border is convex, and is roughened as though for cartilaginous attachment. Its superior portion forms a convex continuum with the scapula. The direct line or external face of the scapula extends in a nearly plane surface to the glenoid cavity, embracing a perforating foramen above the latter, precisely as in the *Pelycosauria*. Its surface is continuous anteriorly with a wide expansion forwards, whose fine inner border is continuous with that of the coracoid. This plate doubtless

includes a third element, but its borders are not preserved, on account of the obliteration of the sutures. It is probably *epicoracoid*, as in the Pelycosauria.

From the foregoing, it is apparent that in several groups of Permian reptiles and in the primitive Eryops, there is considerable evidence to support the theory of a third coracoidal element—the epicoracoid in front of the precoracoid.

The following table shows the presence or absence of these several coracoidal parts in fossil and living forms according to the interpretation of the homology of the coracoid herein set forth.

	METACORACOID	PRECORACOID	EPICORACOID
Eryops.....	*	*	*
Moschops.....	*	*	*
Dimetrodon.....	*	*	*
Diadectes.....	*	*	*
Seymouria.....		*	
Varanosaurus.....		*	
Sphenodon.....		*	*
Lizards.....		*	*
Alligator.....		*	
Monotreme.....		*	*
Marsupial fetus.....		*	*
Marsupial adult.....		*	
Man.....		*	

* = element is present.

While the above table is not in any sense a phylogenetic one, it shows that in several groups of Permian fossils, relatives to the ancestors of the mammals, three coracoidal elements were present, and by the dropping out of either the most posterior element (*metacoracoid*) or the most anterior element (*epicoracoid*), or both of these elements, all the variations met with from Permians to man are explicable.

The relations and homologies here set forth will stand regardless of what disposition is finally made of Gregory's "epicoracoid or third coracoid element," for the homologies of the coracoid all hinge upon the precoracoid as the constant and vital factor in the phylogenetic succession.

The epicoracoid may be, for all anyone has shown to the contrary, merely a neomorph, like the subcoracoid, with no morphological significance. Regardless, then, of the fate of the epicoracoid, the following homology apparently is established, namely, that *the precoracoid of Permians = coracoid of living reptiles = coracoid of monotremes = coracoid of marsupials = coracoid process of man.*

It is at once apparent that the precoracoid of Permian reptiles is the constant factor in the situation. Since, as shown by Williston, this element (precoracoid) is the one preserved and known as the coracoid of *Sphenodon*, lizards, and the alligator, the term coracoid is correctly applied only to the homologues of the precoracoid. Gregory and the author have argued for the homology of the girdles of *Sphenodon* and lizards with that of the monotremes, and Broom and the author have shown that the conditions in the monotremes are directly comparable with the fetal girdle of the marsupials, therefore, the two elements of the girdle in the fetal marsupial (coracoid and epicoracoid) are homologous with the same two elements in the lizard and *Sphenodon*. But these elements of *Sphenodon* and the lizards are demonstrated by Williston and Case to be the homologues of the precoracoid and cartilaginous third element (epicoracoid) of Permian reptiles. Therefore, again, the two elements of monotremes and fetal marsupials are homologues of the precoracoid and cartilaginous epicoracoid of Permian reptiles, and not to the precoracoid and metacoracoid, as assumed by Watson and Broom.

In the fetal marsupial the epicoracoid is embryonic only, the coracoid aborts except for a small rudimentary process attached to the scapula, which is undoubtedly the homologue of the same-named element in higher mammals and man. Therefore, once again, the coracoid process of man is a precoracoid and the homologue of the precoracoid of fossil reptiles.

It may be objected that the precoracoid of Permian reptiles, and its homologue in living reptiles, carried a foramen and nerve. This is not present in monotremes, and we must assume it to be lost here. This is not a serious objection, as the foramen is also absent from the coracoid of many birds, which coracoid is without question the homologue of the precoracoid.

Also it may be pertinent to ask, if the coracoid process of placental mammals is the posterior element of Permians, how did it get to the anterior side of the glenoid? It is hard to imagine any rotation or migration of this element which would bring it from a position distinctly posterior of the glenoid to its present distinctly anterior position.

THE SUBCORACOID

The subcoracoid center of placental mammals has been homologized by Howes ('93), Lydekker ('93), and others to the metacoracoid of Permian reptiles. They regard the subcoracoid center of mammals as the vanishing vestige of the metacoracoid. Gregory ('15) and also Williston formerly accepted this homology, but Gregory ('18) has reconsidered this element and now believes it to be a neomorph or cartilaginous epiphysis and without morphological significance.

Hanson ('19), in studying this subcoracoidal element in the pig (an animal lacking the coracoid process), came to the conclusion that this center of ossification in the pig was an epiphysis.

The subcoracoid always occupies the anterior portion of the glenoid, just behind the coracoid process. The posterior part of the glenoid in mammals is formed by the lower end of the scapula. To accept the subcoracoid element as the last remaining rudiment of the metacoracoid, it would be necessary to assume that in some way there was a rotation of the scapula so that the posterior side of the glenoid in Permian reptiles is now the anterior side of placental mammals, or else in some manner that this center has migrated across the glenoid cavity anteriorly to its present position. Either of these explanations puts our credulity under a rather heavy strain.

Gregory and Camp ('18) also point out in this connection that the subcoracoid "is located at the anterior end of the glenoid ligament where the latter is continuous with the tendon of the biceps . . . as the intrascapular position of part of the biceps is undoubtedly a neomorph in the placentals, we suggest that the appearance of a subcoracoid is also a neomorph."

Broom was the first to suggest that the subcoracoid was an epiphysis, and not part of the coracoid complex.

SUMMARY

1. It has been shown by Broom for Australian marsupials and the author for the American opossum that in the embryo and fetus, the shoulder-girdle consists of a scapula, a clavicle, and two coracoidal elements, one of which, the posterior, extends from the scapula to the sternum and is comparable directly with the coracoid of monotremes. The anterior element of the marsupial fetus is a broad fan-shaped sheet of mesenchyme, of short duration in embryonic life, and is the homologue of the epicoracoid of monotremes.

2. Development shows that the posterior of the two coracoidal elements of the fetal marsupial girdle becomes the small coracoid process attached to the scapula in the adult, which process undoubtedly is homologous with the same-named process in man. This gives a clear line of relationship from the coracoid process of man to the posterior element in the girdle of the monotremes.

3. Gregory and the author have maintained that the conditions in the monotreme girdle are so clearly reptilian in character and approximate so closely in every respect to the structure of the girdles in *Sphenodon* and the lizards, that genetic relationship and homology exists between them.

4. Williston has practically demonstrated that the coracoid of living reptiles is derived from the anterior bony element (precoracoid) of Permian reptiles.

5. Therefore, if the coracoid process of man is the same element as the posterior coracoid of monotremes, and this latter is directly comparable with the posterior of the two coracoids of *Sphenodon* and lizards, which is in turn a derivative of the precoracoid of Permian reptiles, then the coracoid process of man equals the anterior bony element of Permians, and *the precoracoid is the true coracoid*.

6. The subcoracoid of placental mammals is not a coracoid element at all, but an epiphysis, and does not enter into the problem of the coracoid.

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ABBREVIATIONS

<i>Ac</i> , acromian	<i>ICl</i> , interclavicle
<i>Cl</i> , clavicle	<i>MCr</i> , metacoracoid
<i>Cleith</i> , cleithrum	<i>PCr</i> , precoracoid
<i>Cr</i> , coracoid	<i>PSt</i> , presternum
<i>ECr</i> , epicoracoid	<i>Sc</i> , scapula
<i>Gl</i> , glenoid	<i>SSc</i> , suprascapula
<i>Hu</i> , humerus	<i>St</i> , sternum

PLATE 1

EXPLANATION OF FIGURES

1 Transverse section of the shoulder-girdle and sternum of a 7.5-mm. embryo of *Didelphys virginiana*. Scapula and coracoid continuous at glenoid. Coracoid extends to and unites with the sternum. Series 924, slide 3, section 35, Harvard Embryological Collection.

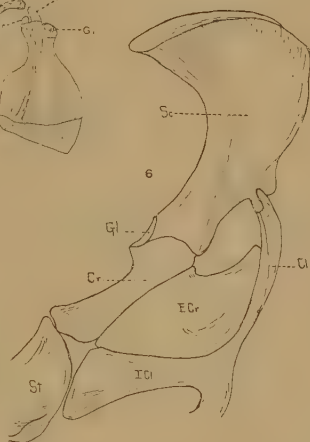
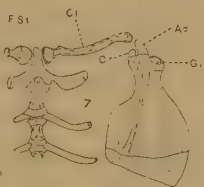
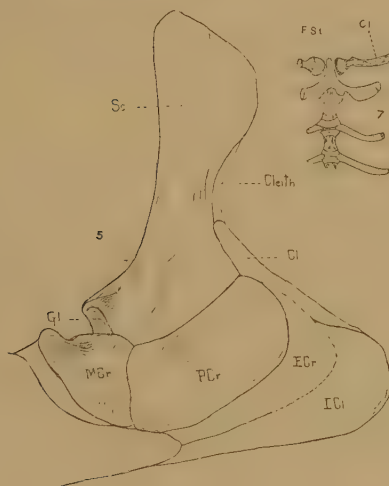
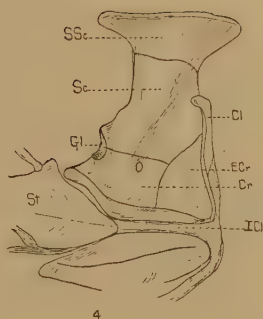
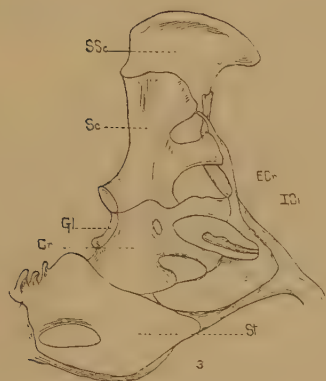
2 Frontal section of the shoulder-girdle and sternum of 11.5-mm. embryo of *Didelphys virginiana*. This section shows the connection of the large coracoid with the sternum, but is cut in such a plane as to exclude the scapula. Series 6127, slide N, section 5, Harvard Embryological Collection.



PLATE 2

EXPLANATION OF FIGURES

- 3 Shoulder-girdle of iguana. Modified after Parker and Gregory.
- 4 Shoulder-girdle of Sphenodon. Modified after Gregory and Camp.
- 5 Shoulder-girdle of Permian Moschops. After Gregory and Camp.
- 6 Shoulder-girdle of the monotreme, Ornithorhynchus.
- 7 Shoulder-girdle and anterior part of sternum of the marsupial *Petrogale xanthopus*. Note small rudimentary coracoid process and compare with coracoid in figures 1 and 2.



Resumen por el autor, Homer B. Latimer.
Universidad de Nebraska.

Peso de las vísceras en la tortuga.

Veintiún machos y una hembra de la tortuga de Cumberland (*Chrysemis elegans*) fueron empleados en el presente trabajo. Después de cloroformizados se pesaron, disecándoles a continuación y extrayendo las vísceras, que se pesaron, en frascos de pesar con tapón de vidrio, en una balanza química que podía apreciar diferencias de una décima de miligramo.

El peso ordinario de las vísceras expresado en tantos por ciento del peso total es el siguiente: el corazón, 0.31; el bazo, 0.21; los pulmones y tráquea, 1.07; el tubo digestivo sin su contenido, 6.23; el hígado, 5.43; el páncreas, 0.15; los riñones, 0.31; y los testículos 0.23 por ciento, o sea un total de 13.74 por ciento del peso total del cuerpo.

Cuando se emplearon los pesos absolutos del cuerpo y de cada órgano para determinar el coeficiente de variabilidad, el autor halló que el peso del cuerpo posee un coeficiente menor que el de cualquiera de los órganos. Los órganos que poseen un coeficiente de variabilidad menor son generalmente los órganos con un coeficiente mas alto de correlación con el peso total del cuerpo. Naturalmente, los coeficientes de variabilidad de los órganos son mas pequeños cuando en vez de los pesos absolutos se emplean los pesos en tantos por ciento. Estos últimos se obtienen reduciendo los absolutos a un por ciento del peso total del cuerpo.

Translation by José F. Nonidez
Cornell Medical College, New York

THE WEIGHTS OF THE VISCERA OF THE TURTLE¹

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The frequent use of the turtle for laboratory purposes and the lack of quantitative data on the size of the turtle viscera has made it seem worth while to determine the weights of the viscera of the turtle. Another thing which suggested this problem was the question of the effect of the weight of the turtle shell on the percentage weights of the organs. The only published quantitative work on the turtle viscera of which I am aware is the report of Welcker and Brandt ('03) upon a single female specimen of *Testudo graeca*. The brain and spinal cord of each turtle were removed, measured, and weighed, and this data will be combined with similar data from other forms and published later.

MATERIAL AND METHODS

The specimens used in this investigation were twenty-one male and one female Cumberland terrapins (*Chrysemys elegans*), three Southern musk turtles (*Aromochelys tristata*), one male and two females, and one male specimen of Lesueur's terrapin (*Malacoclemmys lesueurii*). The turtles were killed with chloroform. The small turtles were weighed on a chemical balance sensitive to a tenth of a milligram, the larger turtles, the Cumberland terrapins, were weighed on a laboratory balance sensitive only to a tenth of a gram. The viscera were carefully dissected out and immediately put in ground-glass-stoppered weighing bottles after all the excess blood had been allowed to drain off. The lungs and trachea were weighed together, the trachea being severed at its attachment to the pharynx. The oesophagus was cut away

¹ Studies from the Zoological Laboratory of the University of Nebraska, no. 126.

from its attachment to the pharynx and the large intestine was severed at its opening into the cloaca. The entire tract was removed with as little of the surrounding fat and the mesenteries as possible. The stomach and intestines were opened and the contents removed. What little material there was in the intestine could usually be forced along the intestine by gentle pressure until it could be removed at the end or at one or two incisions. All the other viscera were removed in a similar manner with as little of the mesenteries and fat as possible. The net body weight and the percentage of loss were not determined as they were for the frogs (Latimer, '20), but in other respects the same plan, which was described in the previous paper, was followed in the dissection and weighing of the turtles.

The twenty-two Cumberland terrapins were received from a Chicago dealer, and the fact that but one of the twenty-two was a female is interesting. They were kept in a tank with free access to running water in a room with a temperature slightly below the usual laboratory temperature. The first turtle was killed and studied December 23, 1919, or soon after they were received. The last one was killed January 26, 1920. They received no food during this time, and when killed only small masses of fecal material were found toward the caudal end of the intestines. They all had ample quantities of fat in the mesenteries, showing that they were in good condition.

PERCENTAGE WEIGHTS OF THE VISCERA

Table 1 A gives the total weight in grams of each of the twenty-one male *Chrysemys elegans* and the weights of the viscera of each turtle expressed in percentages of the total body weight. Sections B, C, and D give the same data for the one female *Chrysemys elegans* and for the other turtles. The weights of the digestive tract are for the empty tract. There was so little material to be removed that no correction was made for this in the total body-weight.

Table 2 will facilitate comparisons between the turtles and other species. It shows the averages of the percentage weights

of the various organs of the turtles and the same data for the other forms. The first line gives the average percentage weight of the organs of the twenty-one male turtles (*C. elegans*). The second line gives the averages for the three Southern musk turtles, and the third line the percentage weights of the viscera of the one Lesueur's terrapin. The data for the first three lines are taken directly from table 1. The percentage weights for the *Testudo graeca* are taken from the report of Welcker and Brandt ('03) and are for a single female specimen. The next two lines give the average percentage weights of the organs of the ten male and nineteen female frogs (*Rana pipiens*) from a previous paper (Latimer, '20). The percentages of the rat viscera are those given by Jackson ('13) for one-year-old male white rats. The last line gives the data on the human organs as given by Vierordt ('06). The last column of the table shows the totals of the percentage weights for all the viscera of each species. These were determined from the four-place decimals of the complete tables, and consequently the sums are slightly larger than the sums of the two-place decimals given in this table. It is obviously impossible to place much weight on the figures in the second, third, and fourth lines, for these three lines represent altogether but five specimens.

In comparing the twenty-one male turtles with the frogs it is apparent that each of the organs of the turtle is heavier than the same organ of the frog, with the exception of the heart and the kidneys.

Heart. The heart forms a smaller percentage weight in the turtles than in any of the other forms. Joseph ('08) suggests that the relative size of the heart is correlated with the activity of the animal. This would place the turtle at the bottom of the list as far as activity is concerned, and the *Chrysemys elegans* would be more active than the other three species of turtles, if we may be permitted to judge from the very small numbers. The percentage weights of the heart for the frog, the rat, and the human are nearly the same.

Spleen. The spleen is the most variable organ not only in comparing the eight species listed in this table, but in comparing

TABLE 1
Total weight in grams of the turtles and the percentages of the individual organs

NUMBER	TOTAL BODY WEIGHT	HEART	SPLEEN	LUNGS	DIGESTIVE TRACT	LIVER	PANCREAS	KIDNEYS	GONADS
A. Male turtles, <i>Chrysemys elegans</i>									
	grams								
6	936.8	0.2891	0.1104	1.8360	6.1631	5.5489	0.1079	0.3521	0.3336
7	739.3	0.3311	0.1613	1.7570	6.5579	4.1323	0.1273	0.3078	0.3225
8	847.9	0.2870	0.3455	1.0438	5.9557	7.3079	0.1852	0.3757	0.2560
9	899.9	0.2944	0.1387	0.9932	6.0045	5.0525	0.1322	0.2761	0.1970
10	751.5	0.3504	0.2126	0.9613	5.4584	4.6881	0.1347	0.3225	0.2100
11	1001.1	0.3220	0.1504	0.7779	5.9414	5.2603	0.1709	0.2729	0.2300
12	688.9	0.3480	0.2445	1.4588	6.0508	6.5847	0.1609	0.2822	0.1934
13	867.5	0.2857	0.2913	1.1537	6.8020	6.9162	0.2781	0.4389	0.2021
14	796.2	0.3204	0.2887	0.9770	6.6279	5.0136	0.1214	0.2708	0.3278
15	803.0	0.2940	0.1470	0.9095	6.3575	4.4288	0.1333	0.3165	0.2558
16	801.9	0.3405	0.1509	0.9838	7.2405	4.4117	0.1850	0.3455	0.4714
18	887.3	0.2838	0.1659	0.7918	7.6388	4.5727	0.1615	0.3215	0.2196
19	973.2	0.3336	0.3814	0.8635	5.9701	6.0895	0.1573	0.3383	0.2051
20	784.4	0.3223	0.1618	0.8405	5.7153	5.1820	0.1550	0.3224	0.2250
21	922.3	0.3431	0.2377	1.3070	5.7168	5.5299	0.1535	0.3018	0.1265
22	938.1	0.2753	0.3109	0.8520	6.2321	5.8579	0.1423	0.3060	0.2125
23	708.9	0.4003	0.2529	1.2937	5.8309	6.4449	0.1924	0.2833	0.3192
24	799.5	0.3645	0.1787	0.9879	6.1119	5.9328	0.1391	0.3447	0.1743
25	848.7	0.3240	0.2099	0.9165	6.0510	5.6323	0.2000	0.2979	0.1263
26	706.5	0.2952	0.1661	0.9383	6.3290	4.4632	0.1437	0.3171	0.1491
27	932.7	0.2504	0.2282	0.8934	6.0870	5.0702	0.1212	0.2703	0.1198
Average		0.3169	0.2159	1.0732	6.2306	5.4343	0.1573	0.3173	0.2323
Standard deviation		0.0344	0.0723	0.2901	0.5017	0.5123	0.0364	0.0395	0.0828
Coefficient of variability		10.839 ±1.273	33.464 ±3.853	27.030 ±2.915	8.052 ±0.843	9.427 ±0.989	23.132 ±2.476	12.439 ±1.131	35.658 ±4.158

B. Female *Chrysemys elegans*

17	865.3	0.3065	0.4699	0.8402	7.3181	5.9237	0.3269	0.3592	0.1295
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C. One male (no. 2) and three female (nos. 3 and 4) *Aromochelys tristycha*

3	85.0635	0.2138	0.0247	0.9757	3.6992	2.6441	0.1328	0.0783	0.4039
4	91.5935	0.3025	0.0463	0.9347	3.3001	2.0188	0.1533	0.2387	0.2983
2	116.1635	0.3499	0.0289	0.8625	3.1655	2.5549	0.1360	0.5047	0.1073
Average		0.2887	0.0333	0.9236	3.3882	2.4059	0.1407	0.2739	

D. Male *Malacoclemmys lesueurii*

5	254.3	0.2481	0.1896	1.1411	3.1191	3.7596	0.1362	0.2427	0.0681
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the individual twenty-one male turtles and the twenty-nine frogs. It is thirteen times heavier in the rat than in the three musk turtles.

Lungs. The weights of the lungs in terms of percentage of the total body weight are heavier in the turtle than in the frog. In weighing the turtle lungs the trachea is included. This might account for the difference, but the turtle *lung* is a more complicated structure than the simple sac-like lung of the frog. No separate weighings of the trachea were made.

Digestive tract. The digestive tract in the Cumberland terrapins, *Testudo graeca*, and the white rat is much heavier than the

TABLE 2

Showing the average percentages of the viscera for the following species

	HEART	SPLEEN	LUNGS	DIGES- TIVE TRACT	LIVER	PAN- CREAS	KID- NEYS	TOTALS
<i>C. elegans</i>	0.31	0.21	1.07	6.23	5.43	0.15	0.31	13.74
Musk turtle.....	0.28	0.03	0.92	3.38	2.40	0.14	0.27	7.45
Lesueur's terrapin.....	0.24	0.18	1.14	3.11	3.75	0.13	0.24	8.83
Test. <i>graeca</i>	0.23	0.10	1.71	5.68	5.78	0.14	0.62	14.26
Male frogs.....	0.43	0.18	0.85	3.50	2.80	0.09	0.43	8.31
Female frogs.....	0.47	0.16	0.76	3.77	2.88	0.09	0.47	8.63
White rat.....	0.45	0.39	0.93	5.1	4.42		0.95	12.25
Human.....	0.46	0.25	1.50	2.06	2.75	0.15	0.46	7.63

percentage weights in the other forms. The lower percentages in the frogs, the musk turtles, and Lesueur's terrapin may have been due to the fact that they were kept in the laboratory for some time before being killed. The Cumberland terrapins were kept in the laboratory for only a little over one month, and that was during the winter time, while the frogs and the other turtles were kept for a longer time and during the summer. It is interesting to note that the percentage weight of the human digestive tract is the lowest and that of the Cumberland terrapin the highest, or a little over three times the percentage of the human digestive tract.

Liver. The variation in the percentage weights of the liver in comparing one form with another seems to parallel the varia-

tion in the digestive tracts. The human, the *Testudo graeca*, and Lesueur's terrapin are the only forms in which the liver is heavier than the digestive tract. Only five of the twenty-one male turtles had a liver with a heavier percentage weight than the digestive tract.

Pancreas. The pancreas forms nearly the same per cent in all forms except the frogs, where it is much less.

Kidneys. The kidneys show a marked variation, the kidneys of the rat being 3.95 times heavier than the kidneys of the Lesueur's terrapin. The kidneys of the three terrestrial forms, the rat, the human, and the Greek tortoise, are heavier than the kidneys of the aquatic forms. The adrenals were included in the weights of the kidneys of the turtles which I weighed, and of the frogs.

A comparison of the sums of the percentage weights of the viscera of the turtle (*C. elegans*) and the frogs is interesting, the former being 1.6 times heavier than the latter. This means that either the organs of the turtle are relatively larger than those of the frog or that the better-developed musculature or other parts of the frog more than compensate for the shell of the turtle. The sum of the percentages for the human most nearly resembles the sum of the percentages of the musk turtles, which were undoubtedly undernourished, due to their prolonged period in the laboratory, and the normal healthy rats resemble more closely the sum of the percentages of the turtle. If we omit the one specimen of the Greek tortoise, we find the viscera of the Cumberland terrapin the heaviest, with the weights of the viscera of the white rat a close second.

COEFFICIENTS OF VARIABILITY

In table 3 are shown the coefficients of variability of the percentage weights of the viscera of the twenty-one male Cumberland terrapins and of the ten male and nineteen female frogs. The coefficient of variation and the probable error of the coefficient of variation for the turtles are taken from table 1. The coefficient of variation and the probable error of the coefficient of variation for each organ of the frogs were computed from the

data given in table 2, page 39, of the report of the frog viscera (Latimer, '20), which gives the percentage weights of the viscera of the chloroformed frogs, *Rana pipiens*. In finding the standard deviation, the coefficient of variation and coefficient of correlation and the probable errors of each of these, Pearson's formulae, as given by Davenport ('04), were used. A six-place logarithm table and the table of squares given by Davenport ('04) aided in the computations. All the results were checked.

This table shows the turtle spleen with a coefficient of variation of 33.46 ± 3.85 or four times that of the digestive tract. The frog spleens have a still higher variability, or 71.0 ± 15.1

TABLE 3
Coefficient of variability of percentage weights

MALE TURTLES	MALE FROGS	FEMALE FROGS
Digestive tract 8.05 ± 0.84	Kidney..... 11.5 ± 1.7	Kidney..... 12.9 ± 1.4
Liver..... 9.42 ± 0.98	Digestive tract 12.6 ± 1.9	Liver..... 19.6 ± 2.2
Heart..... 10.83 ± 1.27	Heart..... 13.4 ± 2.0	Lungs..... 20.7 ± 2.3
Kidney..... 12.43 ± 1.31	Liver..... 15.4 ± 2.3	Digestive tract 21.6 ± 2.4
Pancreas..... 23.12 ± 2.47	Lungs..... 17.7 ± 2.7	Heart..... 22.2 ± 2.5
Lungs..... 27.03 ± 2.91	Pancreas..... 22.2 ± 3.5	Pancreas..... 24.5 ± 2.8
Spleen..... 33.46 ± 3.85	Testes..... 47.2 ± 8.5	Ovaries..... 52.1 ± 7.0
Testes..... 35.65 ± 4.15	Spleen..... 71.0 ± 15.1	Spleen..... 64.7 ± 9.6

for the male and 64.7 ± 9.6 for the female frogs. This it will be seen is greater than the coefficient of variation of either the testes or the ovaries of the frog. The low coefficient of variation of the digestive tract of the turtle is noticeable, due possibly to the lack of food for a similar length of time and uniform conditions of temperature and so forth. The kidney, which is fourth in variability in the turtle, ranks first with a variability of 11.5 ± 1.7 in the male and 12.9 ± 1.4 in the female frogs. The pancreas seems to be about the same in all three columns, with a coefficient of variation of 23 for the turtles, 22 for the male frogs, and 24 for the female frogs. The ovaries, as might be expected, show a greater variability than do the testes, and both gonads of the frogs show a greater variation than do the testes of the

turtles. The heart is third in two columns and fifth in the third, the lungs are sixth in order of the increasing coefficient of variability in the turtle, fifth in the male frogs, and third in the female frogs.

Table 4 gives the data for the weights of the organs in grams; A gives the data for the twenty-one male turtles and B for the

TABLE 4

Showing average weights, standard deviations, and coefficients of variability, computed from the actual weights of the organs in grams

	AVERAGE WEIGHT	RANGE	STANDARD DEVIATION	COEFFICIENT OF VARIABILITY
A. Twenty-one male turtles				
	<i>grams</i>			
Body weight.....	839.79	688.9-1001.1	89.685	10.67 $\pm$ 1.12
Heart.....	2.6465	2.0858-3.2462	0.292	11.06 $\pm$ 1.16
Spleen.....	1.8226	1.0341-3.7120	0.699	38.36 $\pm$ 4.54
Lungs.....	8.9475	6.5932-17.2002	2.435	27.22 $\pm$ 3.03
Digestive tract.....	52.3223	41.0200-67.7790	6.901	13.19 $\pm$ 1.39
Liver.....	45.7266	30.5501-61.9637	8.993	19.66 $\pm$ 2.12
Pancreas.....	1.3204	0.9410-2.4125	0.338	25.65 $\pm$ 2.84
Kidneys.....	2.6667	1.9444-3.8076	0.447	16.76 $\pm$ 1.79
Testes.....	1.9356	1.0537-3.7801	0.669	34.58 $\pm$ 4.00
B. Frogs (male and female together)				
Body weight.....	37.4643	24.9564-56.7866	7.056	18.83 $\pm$ 1.72
Heart.....	0.1743	0.0925-0.3473	0.053	30.41 $\pm$ 2.93
Spleen.....	0.0626	0.0176-0.1604	0.037	59.95 $\pm$ 6.96
Lungs.....	0.3003	0.1360-0.5500	0.091	30.57 $\pm$ 2.94
Digestive tract.....	1.4073	0.6623-2.5770	0.489	34.77 $\pm$ 3.43
Liver.....	1.0945	0.5299-2.2951	0.382	34.97 $\pm$ 3.45
Pancreas.....	0.0372	0.0138-0.0670	0.013	35.43 $\pm$ 3.51
Kidneys.....	0.1735	0.0990-0.2762	0.044	25.89 $\pm$ 2.44

ten male and nineteen female frogs taken together. The first column gives the average weights, the second the range or the lowest and highest weight, the third column gives the standard deviation, and the fourth column, the coefficient of variability and probable error of the coefficient of variability for each organ.

In preparing the data for table 3 each individual organ of each specimen was reduced to a percentage weight of the total body

weight of the animal, and so any variation in the weights of the organs due to a variation in the size of the specimen was eliminated. In table 4 the actual weights of each organ were used in the computations. This naturally would make the coefficients of variability larger when the absolute weights are used than when the percentage weights are employed, and is evident from a comparison of tables 3 and 4. It is an interesting fact that the total body weight for both the turtles and the frogs has a lower coefficient of variability than any of the individual organs. Since the entire animal varies less than any of the individual organs, it would seem that there might be some reciprocal relationship between at least some of the organs, but as will be explained below nearly all the correlations are positive (table 5).

The turtle heart has nearly the same coefficient of variability in each table, 10.83 for the percentage weights and 11.06 for the absolute weights. The digestive tract comes second in order of increasing coefficients of variability of the viscera, with a coefficient of 13.19 in this table compared with a coefficient of 8.05 in the preceding table. The kidneys of the frogs still retain their position as the least variable in the list of the organs of the frog, and the spleen is the most variable, having a coefficient of 38.36 for the turtles as compared with 33.46 for the percentage weights. The pancreas and lungs are about the same, but all of the other organs of the turtle have a higher coefficient of variability in table 4 except the testes and for this organ the percentage weights give a coefficient of variation of 35.65 ± 4.15 , and the absolute weights a coefficient of 34.58 ± 4.00 . This is probably due to the fact that there is practically no correlation between the weight of the testes and the total body weight (table 5), and consequently the reduction of the absolute weights of the testes to a percentage of the body weight would not give even as constant a series as the absolute weights themselves. The greatest increase is found in the liver of the turtle. It has a coefficient of variability in the table of percentage weights of 9.42 ± 0.98 and 19.66 ± 2.12 in the table of absolute weights. The liver has a rather close correlation with the body weight (table 5), and so although it is a rather variable organ, reducing its weight to a

percentage of the total body weight reduces its variability. The pancreas and lungs, which are about the same in tables 3 and 4, have a low coefficient of correlation with the total body weight and consequently reducing them to a percentage basis makes but little difference with their coefficients of variation.

The same relationship between the coefficients of variability (tables 3 and 4) and the coefficients of correlation of the various organs with the total body weight (table 5) holds good for the frogs as well as for the turtles. For all of the organs of the frog except the spleen, the coefficients of variability for the percentage weights is less than the coefficients for the absolute weights, and for all of these organs table 5 shows a rather good coefficient of correlation with the body weight. The spleen has a negative correlation of 0.064 and its coefficient of variation for the twenty-nine male and female frogs taken together and using the absolute weights of the spleen is 59.95, but when the percentage weights are used the spleens of the male frogs have a coefficient of variability of 71 and the female a variation of 64.7.

COEFFICIENTS OF CORRELATION

The coefficients of correlation of the absolute weights of the individual organs and the total body weight for the twenty-one male turtles and the ten male and nineteen female frogs, taken in one group, are given in table 5. As has been suggested above, the organs having a close correlation with the total body weight have a lower coefficient of variation when the percentage weights are used than when the absolute weights are employed.

The correlations between the body weights and the individual organs seem to be a little closer for the frogs than for the turtles. The body weight and the pancreas of the frogs have a positive correlation of 0.909, while in the turtles the correlation of the same organ and the body weight is but + 0.391 and the highest coefficient of correlation is + 0.794 for the digestive tract and the body weight of the turtle. The only negative coefficient of correlation of any of the organs with the body weight is that of the spleen of the frog. The testes, lungs, and pancreas of the turtles have very low coefficients of correlation with the body weight.

In table 5 B are shown the coefficients of correlation between some of the organs, both for the turtles and for the male and female frogs. As in the preceding part of the table the correlations are closer for the organs of the frogs, the digestive tract and kidney having a correlation of $+ 0.875$, while the same organs

TABLE 5
Coefficients of correlation

TWENTY-ONE MALE TURTLES	TWENTY-NINE FROGS (MALE AND FEMALE)
A. Correlations with body weight	
Body weight and digestive tract..... $+ 0.794 \pm 0.054$	Body weight and pancreas..... $+ 0.909 \pm 0.021$
Body weight and liver..... $+ 0.632 \pm 0.088$	Body weight and digestive tract..... $+ 0.866 \pm 0.031$
Body weight and kidneys..... $+ 0.613 \pm 0.098$	Body weight and kidneys..... $+ 0.863 \pm 0.031$
Body weight and heart..... $+ 0.535 \pm 0.105$	Body weight and liver..... $+ 0.845 \pm 0.035$
Body weight and spleen..... $+ 0.432 \pm 0.119$	Body weight and lungs..... $+ 0.733 \pm 0.057$
Body weight and pancreas..... $+ 0.391 \pm 0.156$	Body weight and heart..... $+ 0.665 \pm 0.069$
Body weight and lungs..... $+ 0.158 \pm 0.143$	Body weight and spleen..... $- 0.064 \pm 0.124$
Body weight and testes..... $+ 0.089 \pm 0.146$	
B. Correlation of organs	
Liver and spleen..... $+ 0.731 \pm 0.068$	Digestive tract and kidneys..... $+ 0.875 \pm 0.029$
Liver and kidneys..... $+ 0.648 \pm 0.085$	Digestive tract and heart..... $+ 0.858 \pm 0.045$
Liver and pancreas..... $+ 0.626 \pm 0.089$	Digestive tract and liver..... $+ 0.725 \pm 0.059$
Digestive tract and kidneys..... $+ 0.619 \pm 0.090$	Pancreas and liver..... $+ 0.657 \pm 0.071$
Spleen and pancreas..... $+ 0.452 \pm 0.117$	Kidneys and liver..... $+ 0.654 \pm 0.071$
Digestive tract and liver..... $+ 0.362 \pm 0.127$	Kidneys and lungs..... $+ 0.530 \pm 0.090$
Digestive tract and heart..... $+ 0.254 \pm 0.137$	Heart and lungs..... $+ 0.396 \pm 0.105$
Digestive tract and spleen..... $+ 0.253 \pm 0.137$	Pancreas and spleen..... $- 0.108 \pm 0.123$
Lungs and kidneys..... $+ 0.228 \pm 0.139$	Liver and spleen..... 0.0
Lungs and heart..... $+ 0.143 \pm 0.144$	Digestive tract and spleen..... $- 0.025 \pm 0.125$

of the turtles have a positive correlation of but 0.619. The three highest coefficients of correlation between the organs of the turtles are between the liver and spleen, liver and kidney, and the liver and pancreas. The three closest correlations in the frog viscera are the digestive tract and kidney, digestive tract and heart, and the digestive tract and the liver. All the coefficients of correlation are positive for the turtle viscera, although some of them are very low, but for the frog viscera two of the correlations are negative, although low and one is zero. The liver and spleen of the frogs have a coefficient of correlation of zero, and yet for the same organs in the turtle we find the highest correlation of any of the organs, or $+0.731$. The two negative correlations for the frog viscera are the spleen and pancreas and the spleen and digestive tract. Both of these correlations are low in the turtle viscera.

SUMMARY

1. The heart of the male turtles (*C. elegans*) forms 0.31 per cent of the total body weight. It has the lowest coefficient of variability of any of the organs, or 11.

2. The spleen equals 0.21 per cent of the total body weight and is the most variable of the organs, having a coefficient of variability of 38.

3. The lungs which compose 1.07 per cent of the total weight of the turtle have a coefficient of variability of 27.

4. The digestive tract forms 6.23 per cent of the body weight and it has a coefficient of variability of 13.

5. The liver is second largest in percentage weight. It forms 5.43 per cent of the weight of the body and has a coefficient of variability of 19.

6. The pancreas, with a coefficient of variability of 25, forms but 0.15 per cent of the total weight of the turtle.

7. The kidneys form 0.31 per cent of the body weight and have a coefficient of variability of 16.

8. The gonads are less variable than the spleen, for they have a coefficient of variability of 34 and they form 0.23 per cent of the total body weight.

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Resumen por el autor, Otto F. Kampmeier.
Universidad de Illinois.

La circulación colateral en un caso de oclusión completa del orificio
de la vena cava superior.

El orificio de la vena precava y de la mayor parte de la cámara atrial de un corazón humano aparecían obstruidos a consecuencia de la formación de un gran trombus en el atrio derecho, sufriendo dicho trombus una calcificación subsiguiente.

Los cambios resultantes en la dirección y marcha de la corriente venosa pueden resumirse brevemente del modo siguiente: Toda la sangre que vuelve al corazón desde la porción del cuerpo situada sobre el diafragma, excepto la procedente de las venas coronarias, tenía que descender, principalmente por el sistema de las venas azigos, a la cavidad abdominal, donde penetraba en la post-cava. La dirección de la corriente sanguínea en el sistema de las venas azigos, era pues, completamente contraria a la dirección de la misma corriente en el cuerpo normal. Estas modificaciones se han expresado mediante dos esquemas que acompañan al trabajo.

Translation by José F. Nonidez
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THE COLLATERAL CIRCULATION IN A CASE OF COMPLETE CLOSURE OF THE MOUTH OF THE SUPERIOR VENA CAVA

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TWO FIGURES

The case, here described, is that of a negress of middle age, who died of pneumonia in the course of chronic mania. The body was muscular and well nourished; of short stature, being less than five feet in height, it weighed 150 pounds. Surface examination showed a large ulcer on the lower lateral side of the right leg. This character and certain of the internal abnormalities found later led one to suspect syphilis, which diagnosis was subsequently substantiated by the woman's clinical history at the insane asylum¹ where she had been confined. The records revealed that she was a prostitute and a criminal; she committed murder, evidently in a fit of madness, for she was placed in a hospital for mental diseases (1901) and, fourteen years later (1915), was admitted to the asylum for mentally diseased. The clinical data further showed that she had been under syphilitic treatment for years.

During the dissection² of the cadaver, a considerable number of abnormalities were observed, chief of which were those of the heart, to be described presently, also a large fibroid of the uterus, a fairly large lipoma of the back in the lumbar region, softening

¹ Asylum for Mentally Diseased in Wauwatosa, near Milwaukee, Wisconsin. I thank Dr. F. W. Beutler, director of the institution, for looking up the records of the case.

² The dissection was carried out by two of my students, Messrs. J. A. Blair and A. J. Raymond, at the Marquette School of Medicine, Milwaukee, and the figures were copied from my diagrams and prepared for publication by Mr. L. Massopust, the artist of the school.

of a large part of one lobe of the cerebrum (which apparently was not due to postmortem changes following imperfect preservation), marked circulatory deviations, chiefly of the veins, and a number of easily recognizable muscular anomalies, especially of the upper extremity. In fact, the students in the dissecting laboratory claimed "everything was wrong with her."

When the heart³ was examined and studied, the major portion of the right atrium as well as an extensive area of the aortic arch was found to be bony hard. On laying open the chambers of the heart, it was discovered that not only the entire wall of the right atrium, except where the inferior vena cava and coronary sinus entered, but also the entire interatrial septum was composed of a thick, compact 'osseous' tissue. Moreover, this tissue had extended far up through the anterior or ventral wall of the root and arch of the aorta and had invaded the atrioventricular septa partly surrounding the tricuspid and mitral valves. What was most remarkable about this calcified tissue was its great thickness, in many places measuring from 6 to 8 cm. (2 to 3 inches) across. Even though the ventricular walls, except the atrioventricular septa, were for the most part free from the sclerotic deposit, it is a mystery to the writer how the contractions of the heart could have been sufficiently complete to propel the vascular stream throughout the body. The most notable change occurred in the right atrium. Here the sclerotic layer had become so massive as to have occluded the major part of the atrial chamber, shutting off entirely the superior vena cava, but leaving a lumen approximately as wide as that of the inferior vena cava for the passage of the blood from the latter vein and the coronary sinus to the tricuspid portal. To give actual dimensions, the average thickness of the sclerosed interatrial septum was about 3 cm. ($1\frac{1}{4}$ inches), while that part of the bony wall situated between the end or original mouth of the superior vena cava and the remnant of the atrial cavity was no less than 5.5 cm. (slightly more than 2 inches). The latter relations are indicated in figure 1.

³ This specimen, numbered M. 344, is in the Museum of Pathology of Marquette Medical School.

The excessive encumbrance to the heart of the sclerosed areas just pointed out had produced a compensatory hypertrophy of the remainder of the heart, although perhaps not to the degree one should expect. The ventricles were somewhat dilated, their muscular walls were correspondingly thick, and the beginning of the aorta was at least twice as wide as in the normal individual. Besides the pathological features already pointed out, the intima

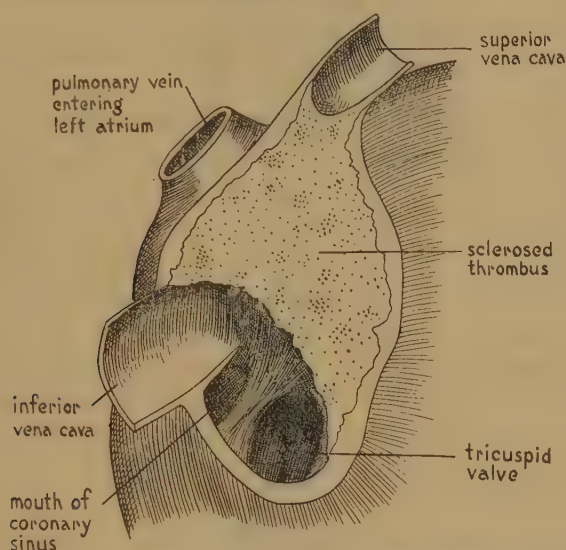


Fig. 1 Semischematic sketch of the right upper portion of the heart, showing one half of the right atrium cut away and illustrating that part of the massive sclerosed thrombus, situated between the orifices of the venae cavae and occluding most of the atrial chamber. Approximately one-half natural size.

or lining of the aortic arch was beset with numerous rough or thin, scaly, bony patches.⁴

A section of the sclerosed wall of the right atrium was prepared for the microscope, which showed definitely, according to Professor McJunkin,⁵ that it represented an organized thrombus.

⁴ Besides the sclerotic patches on the inner surface of the aorta, there were also little pits or depressions and small, parallel ridges, which I believe are considered indicative of syphilis. In a fixed specimen, however, such depressions and elevations must be taken with reserve.

⁵ Prof. F. A. McJunkin, formerly of the Department of Pathology, Marquette School of Medicine, now of the Department of Pathology, Washington University Medical School, St. Louis.

In structure it displayed dense fibrous tissue which had undergone widespread calcification. There were certain peculiarities which suggested syphilitic lesions as a possible initial cause of the thrombus formation. Perhaps it is more likely, however, that the latter began from a secondary infection of some sort, possibly streptococcic in origin, producing a thrombus which arose on the atrial wall itself, or, carried thither from a distant part of the body, became adherent and, gradually growing larger by successive depositions of fibrin, eventually blocked the cavity as demonstrated.

The complete closure of the mouth of the superior vena cava by the atrial thrombus consequently led to extensive modifications in the course and direction of the venous flow from the upper parts of the body to the heart, as illustrated in the diagram, figure 2. These changes may be briefly summarized as follows: 1) All blood returning to the heart from the body above the diaphragm, except that from the coronary veins, was forced to descend to the abdominal cavity, where it discharged into the inferior vena cava. 2) The direction of the blood stream in the azygos system of veins was the exact reverse of that in the normal body. These points are expressed in the diagram (fig. 2) by arrows.

Much of the venous drainage of the head and arm flowed directly into the azygos and hemiazygos veins through the anastomoses of the right and left supreme intercostal and accessory hemiazygos veins with the innominate and vertebral veins. The remainder passed into the superior vena cava, but being unable to enter the right atrium on account of the occlusion of its orifice, it was deflected into the mouth of the azygos vein. From here this blood stream, in conjunction with that coursing through the right supreme intercostal, continued downward in the azygos vein; some of it, however, was turned to the left side through the hemiazygos, thus in direct opposition to the normal course of the flow. All blood passing through the entire extent of the azygos, and most of the blood of the hemiazygos poured via a pair of anastomoses into the inferior vena cava immediately below the diaphragm and at the level of the entrance of the

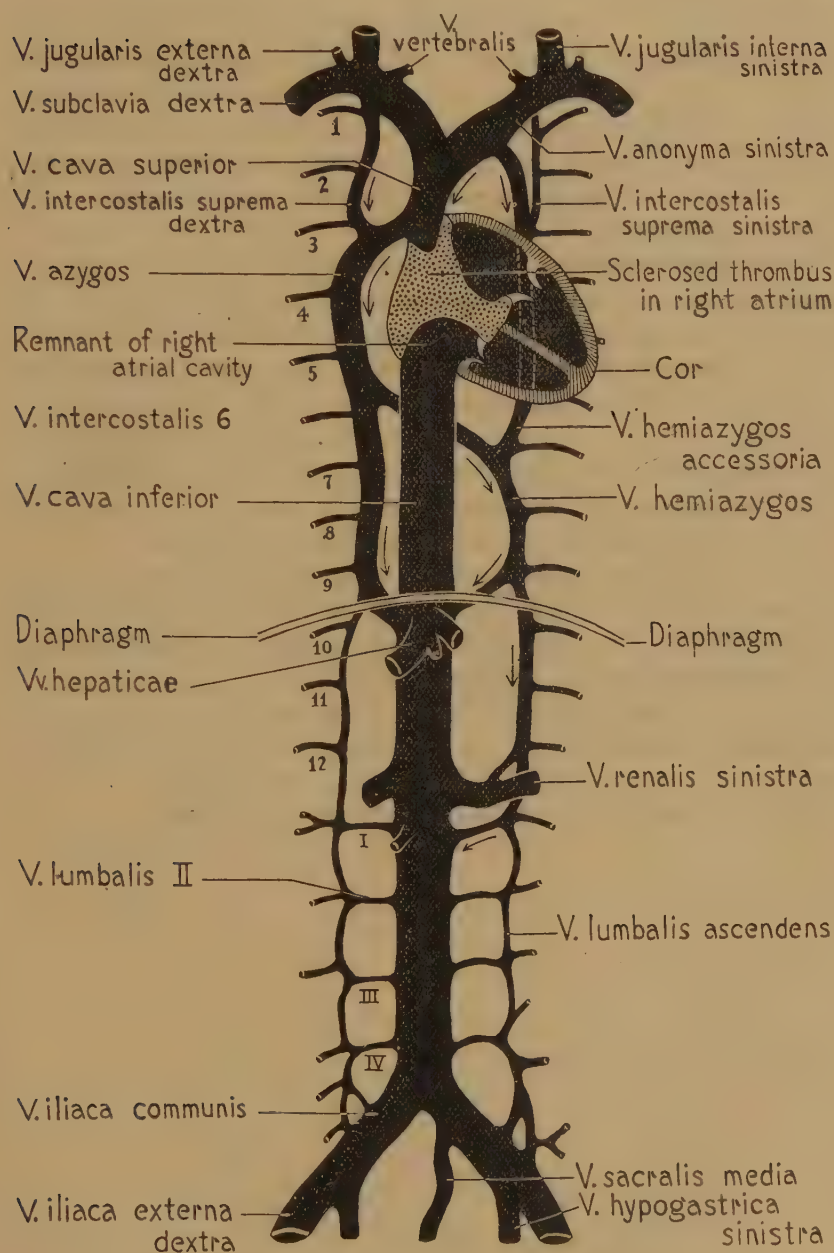


Fig. 2 Diagram showing the closed mouth of the superior vena cava and the resultant modifications in the course and direction of the venous blood stream.

hepatic veins. These anastomoses, which when present in the normal individuals are minute and relatively unimportant, had become very much distended by the demands put upon them. Some of the blood stream of the hemiazygos continued still farther down through the abdominal cavity to empty into the inferior vena cava partly through the left renal vein and partly through the left first lumbar vein.

The valves which are usually assumed to be present in the proximal segment of the azygos vein apparently offered no obstacle to the reversal of the vascular current flowing through it. But such valves do not always exist, and when existent are 'nicht schlussfähig,' according to Spalteholz (*Handatlas der Anatomie*, Bd. 2). Valves which are unable to close the lumen perfectly lose their value in determining the direction of the flow when the caliber of the vessel becomes greatly expanded, as occurred in the case of the azygos under consideration.

Besides the deep and important collateral pathways already mentioned, it is possible that much of the superficial haemal drainage of the thoracic wall, which normally discharged into the axillary, subclavian, and innominate veins through the thoracocolateral, internal mammary and other smaller veins, was in this instance absorbed by the thoraco-epigastric and the superficial and deep epigastric veins to be carried to the femoral and iliac veins and thence to the inferior vena cava.

Resumen por el autor, Edgar D. Congdon.

Un seno paranasal supernumerario.

La cavidad situada medialmente en la región de la fosa incisiva y los canales del mismo nombre de un adulto, presentaba forma ovoidea y poseía una capacidad de unos 3 centímetros. Su pared ósea no era completa por debajo, mientras que por encima se continuaba con las cavidades nasales mediante los cortos canales incisivos.

La formación de esta cavidad debe atribuirse probablemente a la fusión incompleta de los procesos nasales medio y lateral, así como a la actividad formadora de senos del epitelio respiratorio, que ocupa normalmente el extremo superior de los canales incisivos en vías de desarrollo.

Translation by José F. Nonidez
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A SUPERNUMERARY PARANASAL SINUS

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ONE FIGURE

The cavity shown in the accompanying figure was found by a student while making a sagittal section of an adult head. It is medially placed and extends upward from the region usually occupied by the incisive fossa. It is of a regular ovoid form, 9 mm. in height, 5.5 mm. in anteroposterior diameter, and its width is 8.5 mm. if 2 mm. be allowed for the section removed by the saw. Its interior is lined by a smooth membrane which contained a cyst in the right-hand wall 2 mm. in diameter, whose contents was evidently mucoid in nature. A small deposit of similar appearance lay upon the floor of the cavity.

The bony wall of the space contained above a pair of symmetrically placed short passageways, one of which opened into each nasal cavity, where their location and contents of nerves and blood-vessels identified them as the upper ends of incisive canals. At the palatine end bone was lacking over an area several millimeters in diameter, but the gap was filled upon either side of the saw cut by the membrane lining the cavity and the layers investing the bone of the palate. No communication into nose or mouth was found.

Upon microscopic examination the lining membrane proved to be largely fibrous, but covered on the inner surface by a thin layer of columnar epithelium whose precise structure could not be made out because of maceration.

The frequent presence of abscesses in the alveolar process makes it necessary to consider the likelihood of a pathological origin of the cavity. The neighboring bone and teeth seemed sound. The osseous and membranous walls showed no deteri-

oration other than the maceration of the epithelium, and this was judged to have taken place after death.

The region of the incisive fossae was examined in 128 paired and single maxillae in a search for other cavities similar to the one under discussion. The fossae not infrequently bear a slight resemblance to it, as they may be deeper than wide and somewhat narrowed at their inferior end. They are, of course, much smaller and usually of slightly irregular outline. Two of the series, however, show a distinct resemblance to it in the regularity and roundness of their contour, though they differ in being but slightly constricted below. There is a remote possibility, then, that they also may have contained cavities lined with mucoperiosteum.

The continuity of the bony cavity with the incisive canals in our specimen is an indication that it may have been related to them in development. Leboucq ('81) agrees with the observations of Dursey ('69) and His ('01) whose work was accessible only in references from other writers, that the bony incisive canals surround in the embryo an epithelial tube called the incisive duct which is the result of a reopening of a part of the originally free communication between the spaces above and below the palatine processes. For a time after the median nasal and the palatine portion of the maxillary processes have fused, the duct, though closed, is represented by an epithelial cord continuous with the lining of the nose and mouth. The lumen of the incisive duct which develops in this cord usually disappears a second time permanently before birth.

It seems probable that the cavity here described had its beginning either in the incisive ducts or the passageway from which they are derived. If it arose from one or both ducts, it must have undergone a subsequent enlargement, and since it is lined with columnar epithelium which was probably once continuous with the nasal cavity, it would have claim to classification as a paranasal sinus. This interpretation encounters the difficulty that the connection of the bony cavity with both incisive canals must have been the result of a fusion of their lumina—a process rare in sinus development.

It is more probable that the cavity came into existence as a result of a failure in the meeting of the median nasal and the maxillary processes in this region so that a single large space remained where the lower parts of the incisive ducts usually developed. If this supposition is correct, both a change in the form and an increase in the size of the cavity must have occurred, since a space left between three rounded processes would not have an ovoid form and it could not have equalled in size this cavity of the adult bone. A possible difficulty for either explanation is that the columnar epithelium extends close to the



Right half of sinus at (a) exposed by a median sagittal saw cut. $\times 1$

oral surface of the maxilla, while Leboucq found that it gave way in the incisive ducts to the pavement type midway in their course. The exact position of the boundary line is probably not significant, however, since the corresponding transition zone also varies considerably in the nasopharynx.

Works upon palatine malformations and upon the development of the incisive ducts were consulted, including Leboucq ('81), Merkel ('92), Le Double ('96), and His ('01), without finding any reference to a cavity in this region. The studies of the paranasal sinuses by Zuckerkandl ('82), Gruber ('88), Onodi ('07, '08), Underwood ('07), and Shaeffer ('10 and '10 a) do not de-

scribe a sinus here. There is a single record of a similar cavity by Meyer ('13).

In his specimen the position was also medial and the bony wall connected with the osseous enclosures of the nose by short incisive canals, but there was no communication with the oral cavity. The dimensions of the cavity were so considerable (1.6 mm. x 1.35 mm. x 2.2 mm.) that the walls were flattened against various areas of the surrounding compact bone, giving it decidedly the appearance of a sinus. A smooth lining membrane was present. No opening into nose or mouth was found. Professor Meyer concluded that it was a paranasal sinus in a very unusual situation and called attention to Underwood's description ('07) of a sinus similarly placed in the chimpanzee.

The characteristics of the cavity found by Professor Meyer and of the subject of the preceding description are so similar that in the writer's opinion the two must have had a similar origin. The dimensions of the cavity in Professor Meyer's specimen are much greater than possible for an unmodified gap left by the medial nasal and maxillary processes. The probable independence of the two from the nasal cavity at all stages of their developmental history sets them apart from the paranasal sinuses more in appearance than in reality since the evidence points to their origin from a membrane that was once at least in continuity with the nasal lining and similar to it in character.

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Resumen por el autor, Clarence Lester Turner.
Colegio Wooster.

Un medelo de cera de un embrión humano en el estado
presomítico.

El embrión descrito en el presente trabajo es un embrión humano normal en el estado que precede a la aparición de los somitas. El autor le designa con el nombre de "óvulo de Mateer", en honor del Dr. H. N. Mateer, de Wooster College, quien le obtuvo y conservó.

El embrión mide próximamente un milímetro de longitud, y presenta en buen estado de conservación el disco embrionario, amnios, corion saco vitelino y pedúnculo del cuerpo. Es sumamente notable por estar contenido en un óvulo que también encierra un embrión gemelo en vías de degeneración.

La serie de dibujos, trazados con ayuda de la cámara clara, que acompaña al texto representa los contornos de todos los cortes, que pasan por el disco embrionario, amnios, saco vitelino, alantoides y pedúnculo del cuerpo. Los cortes medían 10 micras de espesor, y los dibujos les representan aumentados 50 diámetros. Si dichos dibujos se aumentan al doble de su tamaño mediante la proyección o la fotografía, pueden trazarse sobre placas de cera de un milímetro de espesor, y el modelo así obtenido representará una rescontrucción aumentada uniformemente 100 diámetros en las tres dimensiones.

Translation by José F. Nonidez
Cornell Medical College, New York

A WAX MODEL OF A PRESOMITE HUMAN EMBRYO

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Biological Laboratory of Wooster College

EIGHTY-ONE FIGURES

INTRODUCTION

The presomite human embryo figured in this article has been fully described by Prof. George L. Streeter, of Johns Hopkins University, in a recent monograph ('19) and the twin formation of the same ovum in a shorter article ('19). He has designated the embryo as the Mateer Embryo after Doctor H. N. Mateer, of Wooster, through whose efforts it was preserved. It is not the purpose of this paper to attempt to repeat any of the work done, but to present a series of drawings representing all the sections through the embryo and the yolk sac. Such a series of drawings makes it possible for every laboratory in which the wax-plate reconstruction process can be carried out to have a model of this embryo for study. The series should also prove of value to classes in embryology, even though the plane of sectioning is very oblique.

The writer is greatly indebted to Doctor Mateer, the owner of the embryo, for a loan of the specimen and for his generous consent in permitting this series of drawings to be published. Several models were constructed, and this series of drawings was prepared in the Biological Laboratory of Wooster College.

THE EMBRYO

The age of the embryo was placed by Doctor Streeter at about seventeen days. The embryonic shield is approximately 1 mm. long and 0.75 mm. wide at its greatest width. Both the embryonic shield and yolk sac are surrounded by a thin layer of mesoderm and the entire vesicle is attached to the chorion by the body stalk. All the structures, with the possible exception of the allantois, are apparently quite normal.

A. Embryonic shield

The embryonic shield is oval in shape, but narrows markedly and bends ventrally in its posterior third. The oval portion is not marked by any unevenness, but the narrow posterior third is traversed longitudinally by a shallow primitive groove. At the periphery of the shield the ectoderm is continuous, becoming thin and folding over dorsally to form the amnion.

B. Amnion and amniotic cavity

The line of demarkation between the embryo and the amnion is difficult to distinguish in many of the sections, but the amniotic ectoderm is very thin and is overlaid by mesoderm which binds it loosely to the overlying chorion. Owing to the oblique plane of sectioning, an exaggerated impression of the depth of the amniotic cavity is gained from figure 16. The cavity appears in the reconstruction as a mere cleft except at the extreme posterior end where it comes into contact with the body stalk.

C. Body stalk and allantois

The body stalk, occurring at the posterior end of the yolk sac, is a fairly compact mass of mesoderm attaching the entire vesicle to the chorion (fig. 22, B.D.S.). A few loose strands of mesoderm extend from the body stalk to the chorion, and at one point near the chorion the body stalk is interrupted by a large cavity. Some primitive blood-vessels are found also in the body stalk, but no attempt has been made to represent them in the drawings.

The allantois at its proximal end appears as an evagination of the yolk entoderm and within the next few sections becomes a compact round column of cells. The proximal portion of the allantois terminates abruptly and no trace of it can be found for a few sections after which it reappears as a detached segment. In the reconstruction this detached segment shows a marked constriction.

D. Yolk sac

The yolk sac is much flattened dorsoventrally although its probable normal shape was nearly spherical. As the chorionic vesicle is also flattened in the same direction, it seems likely that both chorion and yolk sac were flattened by their own weight prior to fixing. On the ventral and posterior surfaces of the yolk sac are numerous blood-islands.

E. Chorion

There are two layers present in the chorion, an inner mesodermal layer, which is loose in texture but distinct, and an outer and more compact ectodermal layer. Chorionic villi are attached to the chorionic membrane at intervals. The same layers appear in the villi that are present in the chorionic membrane, the ventral mass consisting of the mesodermal element and the outer layer a covering of ectoderm. A syncytial and an epithelial layer may be distinguished in the ectoderm, but they have not been shown in the figures.

F. Twin vesicle

In figure 30 there occur between the large embryo and the chorionic membrane two smaller vesicles which prove to be parts of a second smaller embryo evidently undergoing degeneration. In the larger of these two smaller vesicles a sphere of ectoderm surrounded by mesoderm can be distinguished. The ectodermal sphere enclosing an amniotic cavity is thickened on one side to form the embryonic ectoderm, while the remainder forms an amnion. The second and smaller vesicle is apparently the degenerating yolk sac of the small twin embryo. Both vesicles are loosely bound to the body stalk and to the chorion by strands of mesoderm.

CONSTRUCTION OF MODEL

The plane of sectioning is represented by the line AB. The sections were made 10 μ thick. A few sections were irregular in thickness or were lost, a number have been twisted and a few

broken into fragments. However, by taking the perfect sections as guides, the imperfect sections may be made to conform to the shape as indicated in the perfect sections. With these few exceptions, the sections are in good condition. All the drawings in this series were made with a camera lucida and all the imperfections are figured as they occur in the sections.

A. Irregularities

The more outstanding irregularities are listed here with the expectation that they will prove useful for corrections during the construction of a model. The irregularities were checked by making a duplicate set of drawings with carbon paper, using one set for the construction of the model and carefully marking the necessary alterations on the other set of drawings.

Section 2 to section 9. The amnion on the right side has collapsed or has been pushed in.

Section 3 to section 15. There is a shrinkage of the mesoderm on the left side of the embryo between the embryonic disk and the yolk sac.

Section 5 to section 17. An indentation in the right side of the yolk sac and the overlying mesoderm is evidently an artifact.

Section 3 to section 20. The embryonic disk is cracked in most of these sections and in a few the parts have suffered a slight displacement.

Section 14 and section 15. Two sections have apparently been lost between these two.

Section 17. This one is 40 μ thick instead of 10 μ thick.

Section 16 and section 17. The left half of the embryonic disk is bent ventrally so as to be out of adjustment.

Section 23. There is a lateral compression in this section which distorts it somewhat. The foregoing section may be taken as a guide.

Section 24. As in section 23.

Section 30. The yolk sac membrane and the overlying mesoderm are shrunken and distorted.

Section 32 and section 33. These are somewhat broken and

the pieces displaced, but the general boundaries of the sections are still evident.

Section 34. The ventral half of the yolk sac has been dislocated toward the left.

Section 35. There are two slight breaks in the walls of the yolk sac.

Section 37. This section is $20\ \mu$ thick.

Section 40. The walls of the yolk sac are broken at the ventral point and are shifted toward the left in the ventral half.

Section 42. The sides of this section are somewhat compressed.

Section 46. This section is bent toward the left in its ventral half.

Section 47. The sides of this section are slightly compressed and the lower half is dislocated toward the left.

Section 48 and section 49. Several sections are missing between these two.

Section 50 to section 81. There are many slight irregularities in the shape of the yolk sac, but the shape may be made out by using the following sections as of normal shape: sections 58, 61, 63, 68, and 73.

B. Magnification

The sections have been cut $10\ \mu$ in thickness so that a magnification of 100 would make the wax sheets 1 mm. in thickness. In the illustrations in this article a magnification of 100 has been used, but the drawings have been reduced one-half for publication. It is suggested that they be stepped up to their original size (twice as large as represented here) when wax sheets of a thickness of 1 mm. may be used.

C. Modeling

A model such as the one illustrated in plate 1 may be constructed by the usual Borns' wax-plate method. A more substantial model which may be handled by students may be constructed by substituting blotting-paper soaked in equal parts of beeswax and soft paraffin for 'wax sheets.

The structures which serve best as guide lines in building the model are the body stalk and the allantois. The posterior margin of the amniotic cavity can also be used to advantage.

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1919 Formation of single ovum twins. Johns Hopkins Hospital Bulletin, vol. 30, no. 342.

EXPLANATION OF PLATE AND FIGURES

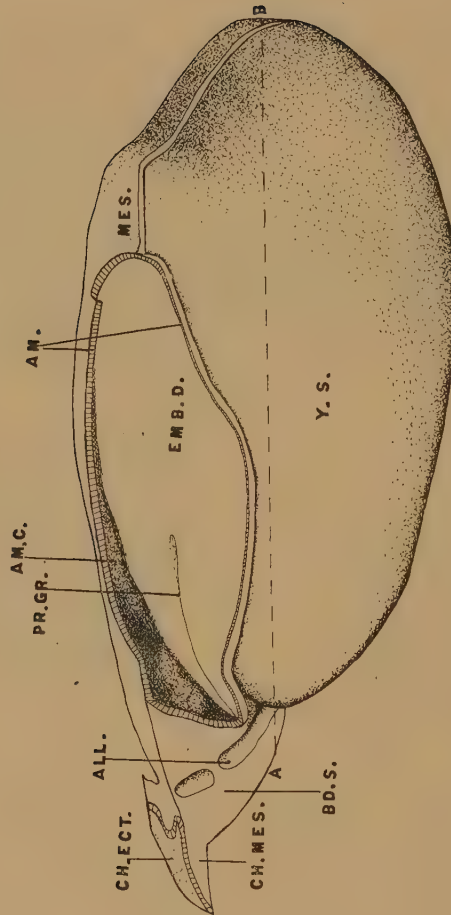
Plate 1. Model, $\times 50$, representing the amnion cut away on the right side exposing the embryonic shield and the amniotic cavity. The body stalk is represented as bisected to show the allantois. The mesoderm overlying the yolk sac is represented as cut away on the right side to expose the yolk sac.

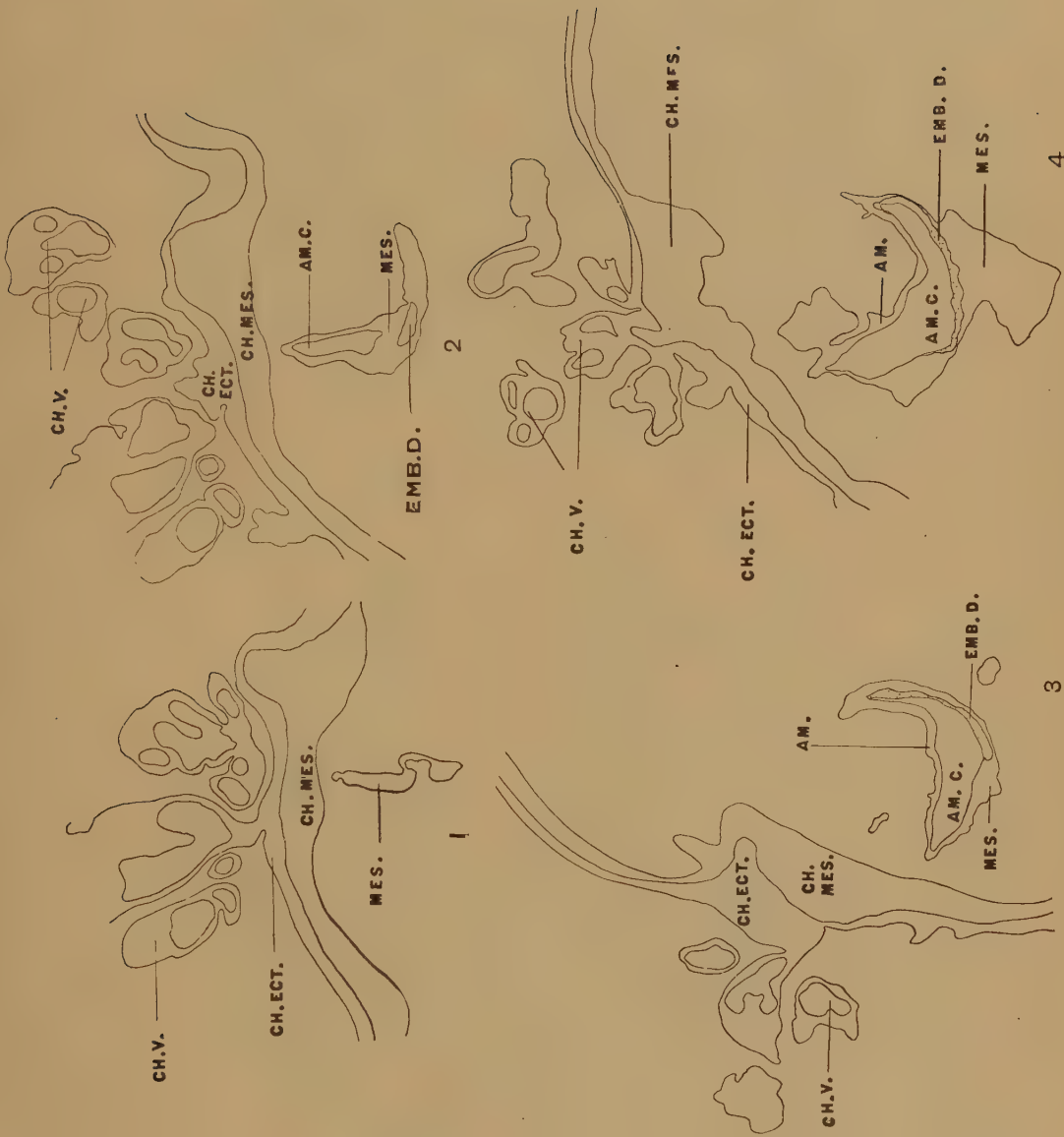
Figs. 1 to 81 This is a series representing all the sections of the ovum in the plane of A B (pl. 1).

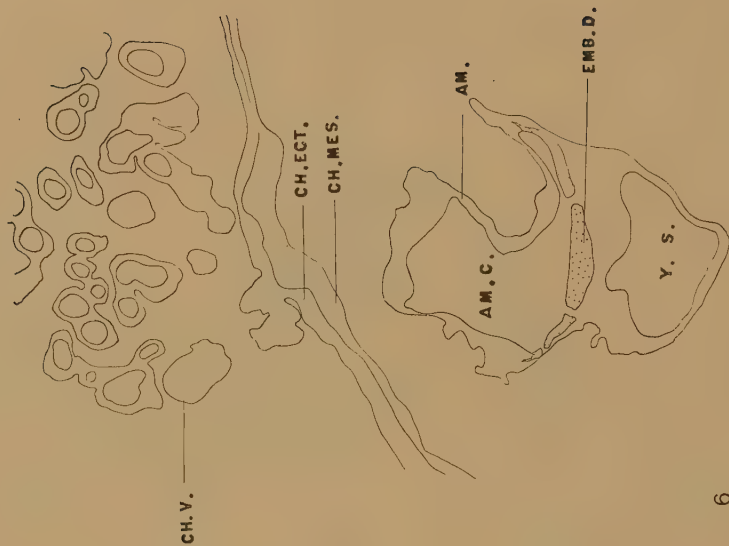
ABBREVIATIONS

ALL., allantois	Y.S., yolk sac
AM.C., amniotic cavity	BL.IS., blood-island
AM., amnion	CH.V., chorionic villus
BD.S., body stalk	TW.V., twin vesicle
CH.MES., chorionic mesoderm	EMB., posterior portion of embryo
CH.ECT., chorionic ectoderm	Y'.S', yolk sac of twin
PR.GR., primitive groove	AM.C.TW.V., amniotic cavity of twin vesicle
PR.ST., primitive streak	EMB.ECT., embryonic ectoderm of twin vesicle
PR.KT., primitive knot	
MES., mesoderm	
EMB.D., embryonic disk	

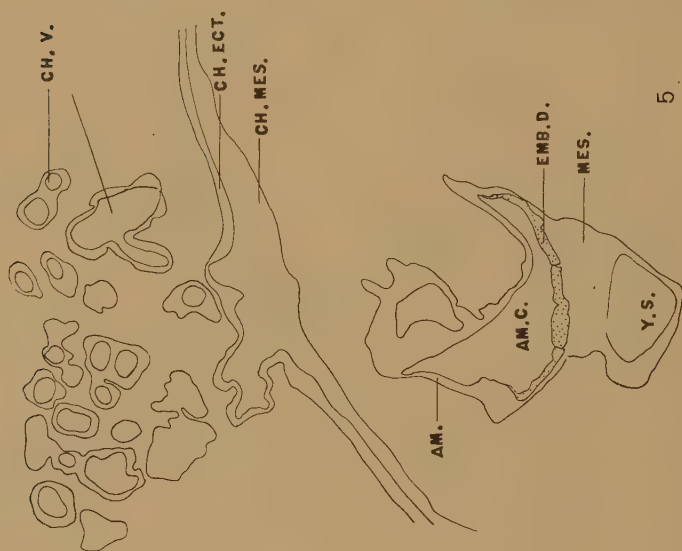
A WAX MODEL OF A PRESOMITE HUMAN EMBRYO
CLARENCE L. TURNER



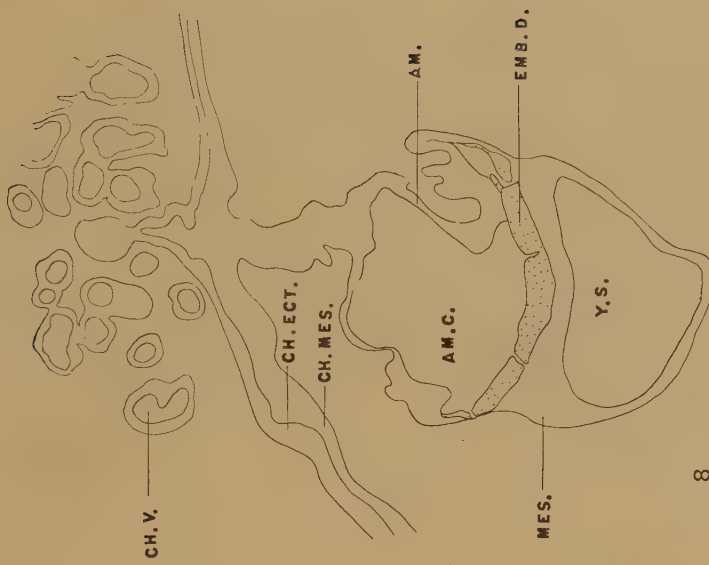




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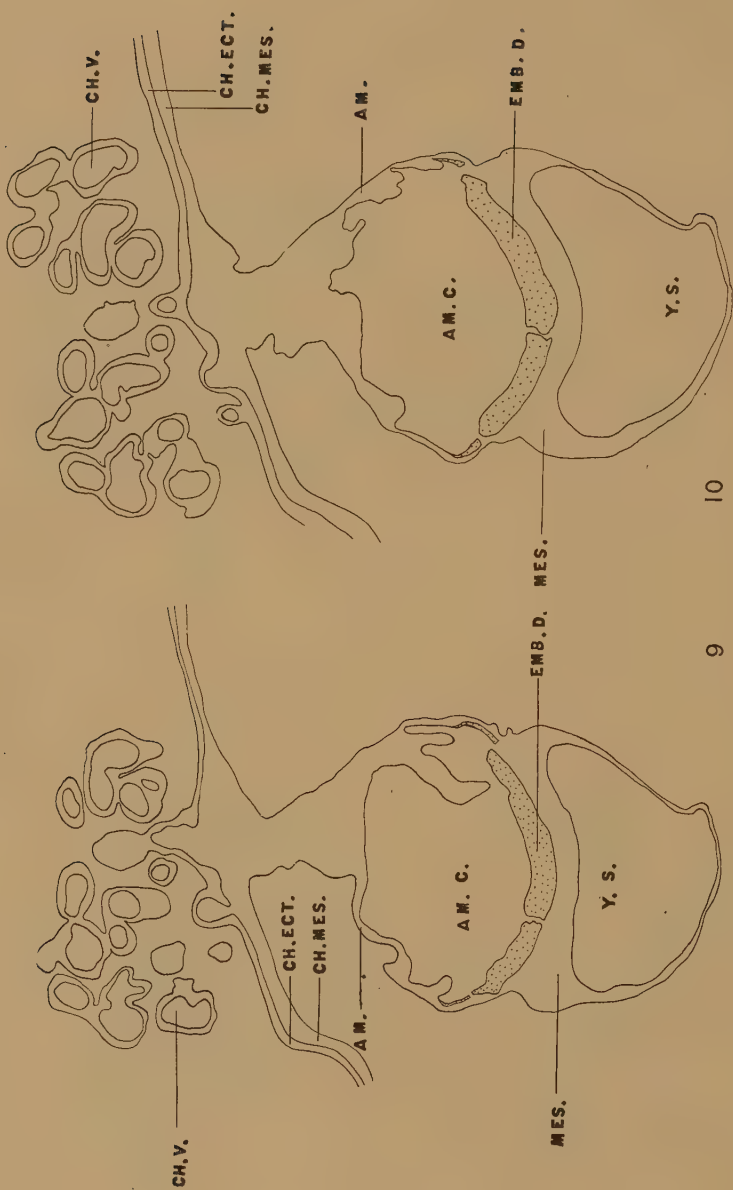
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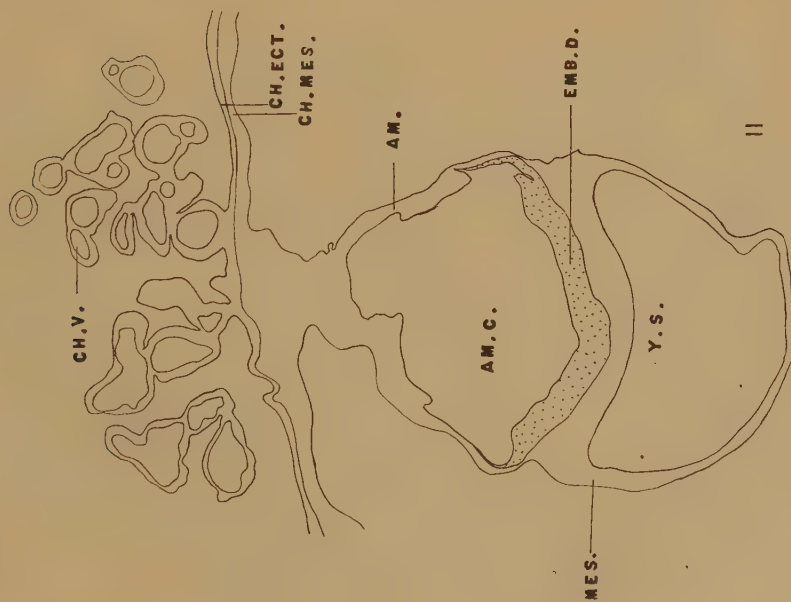


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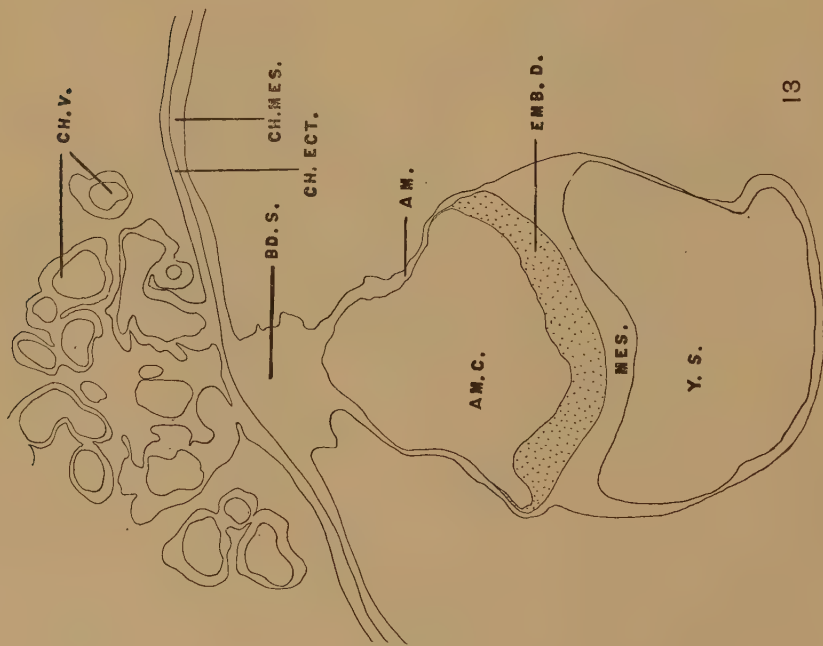




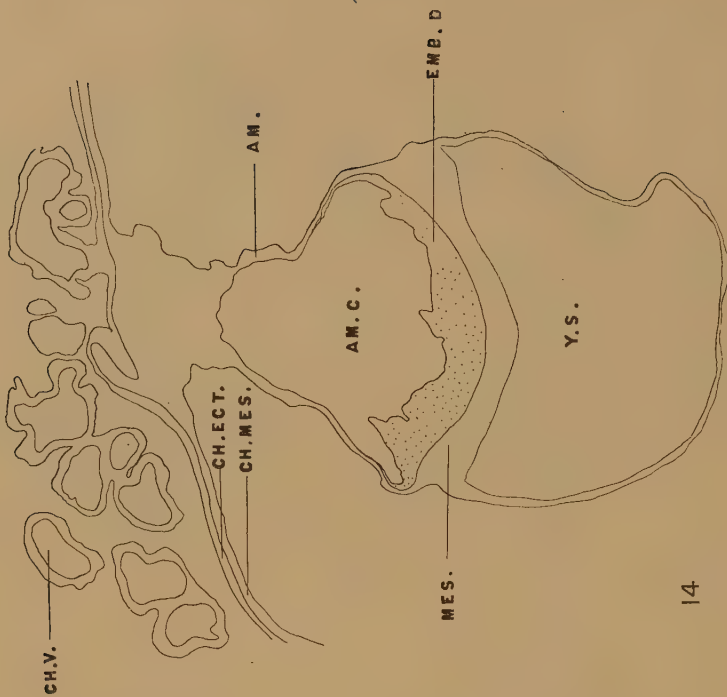
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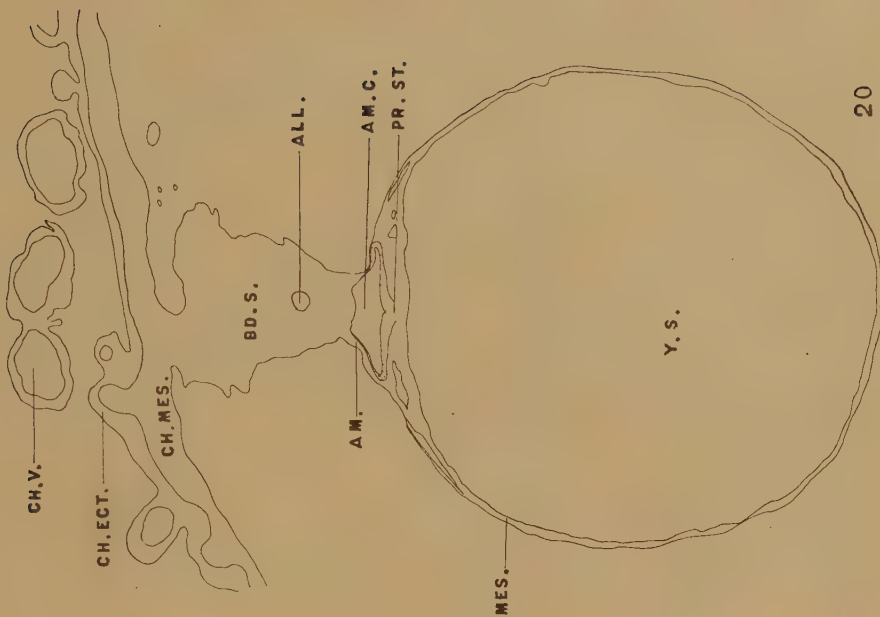
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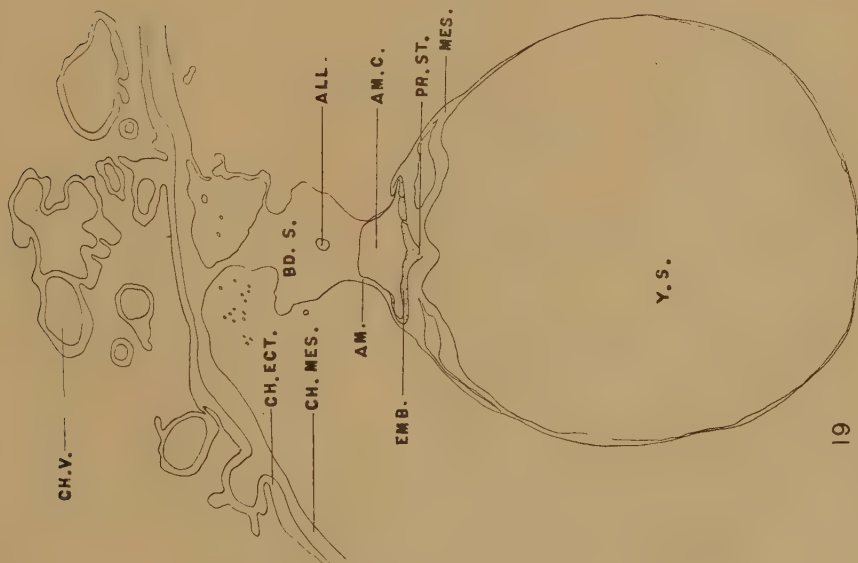
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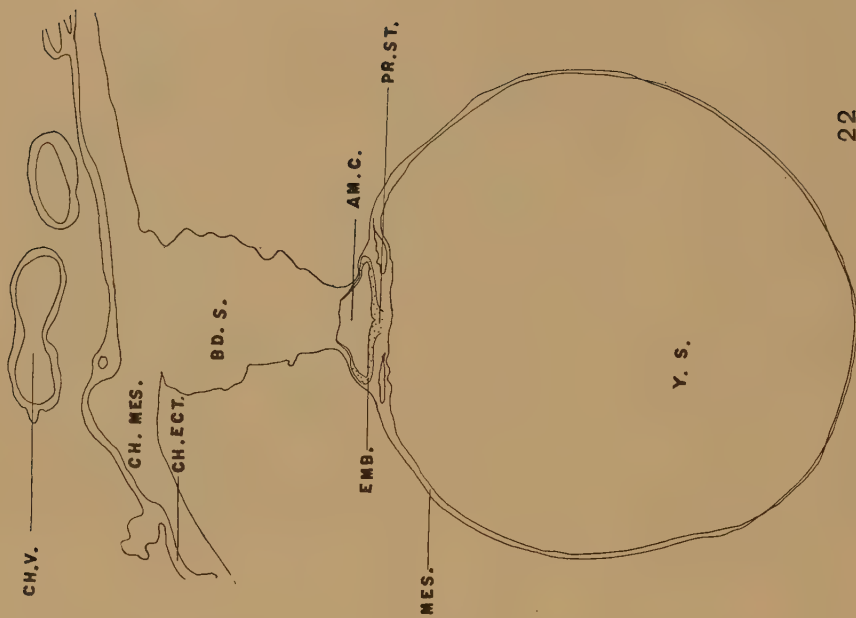




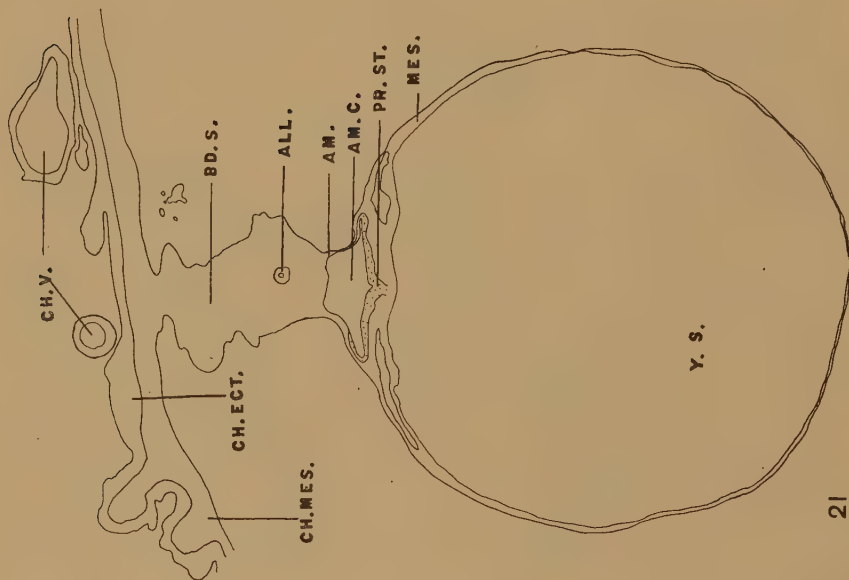
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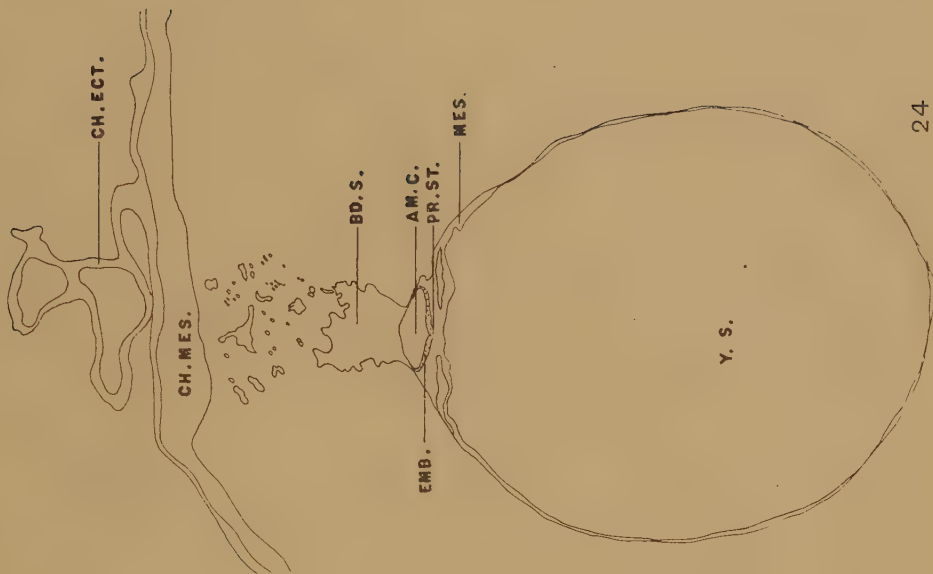
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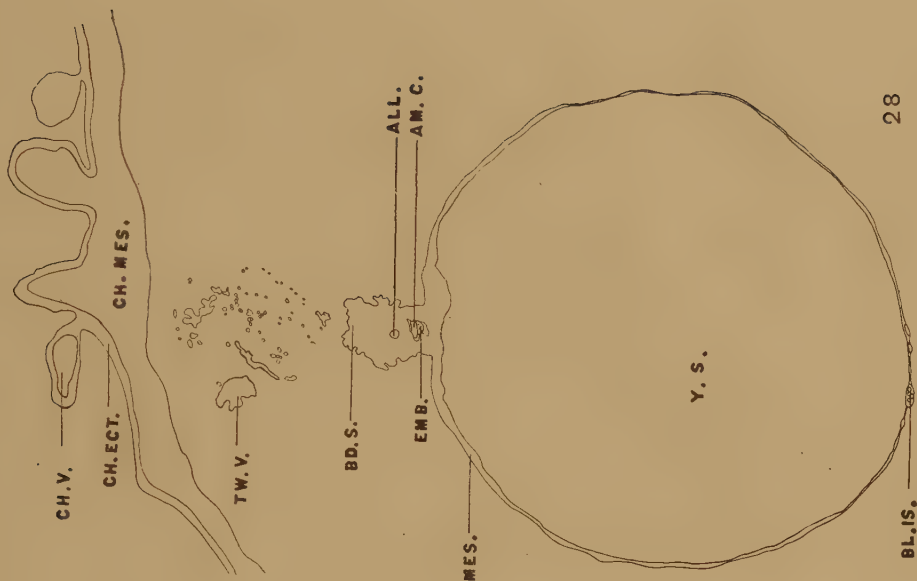


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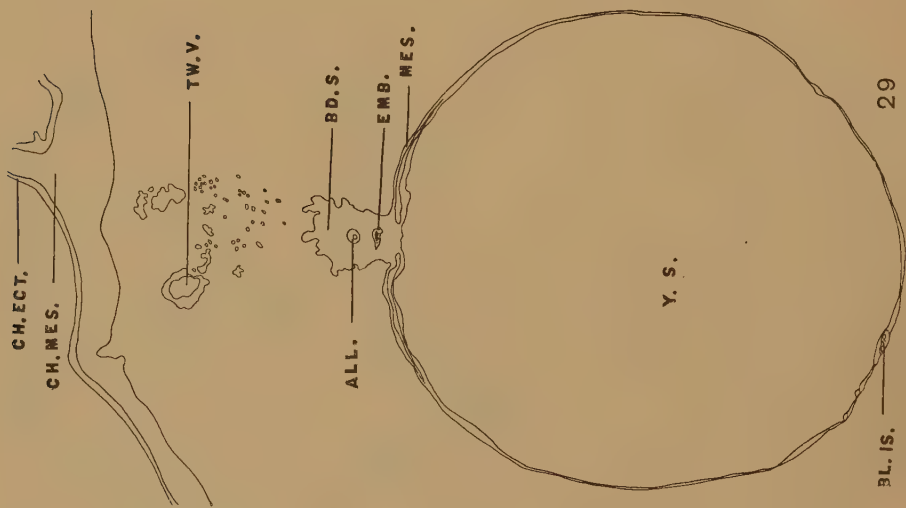


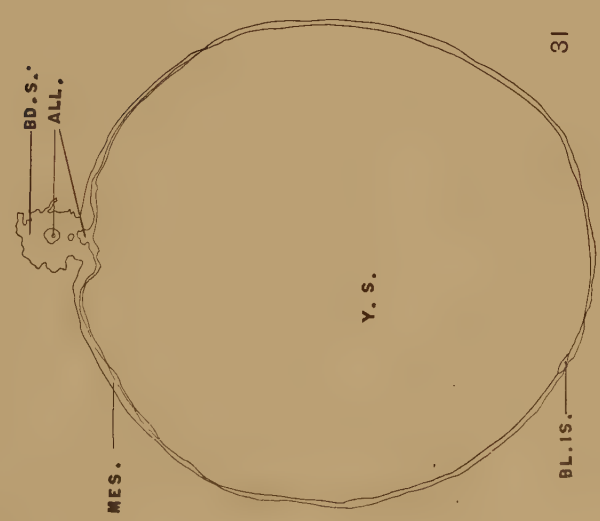


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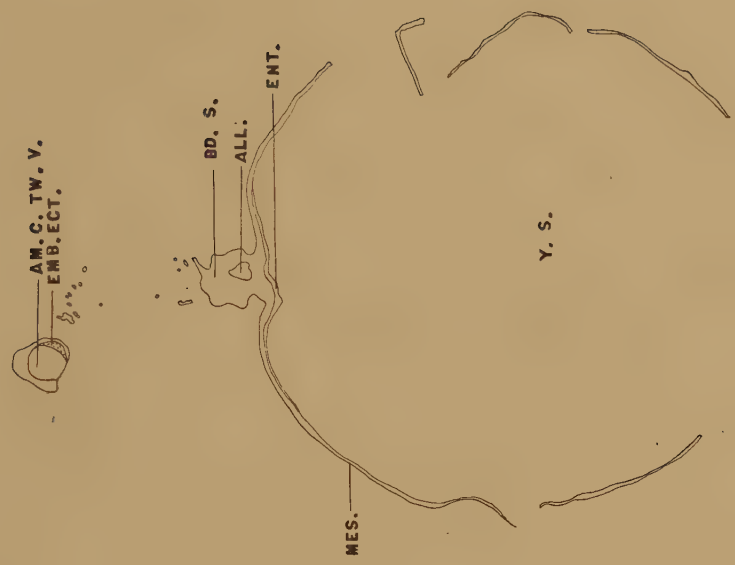


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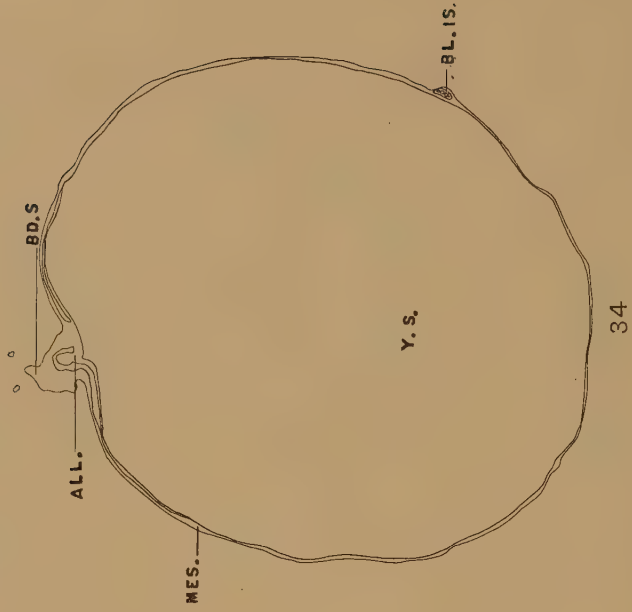


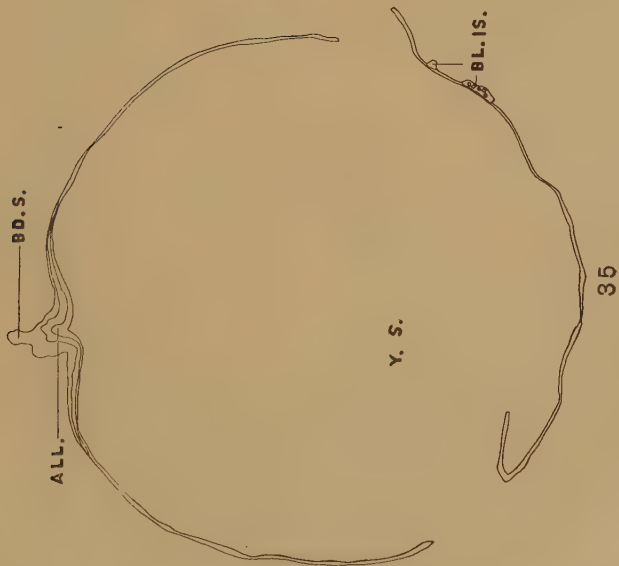


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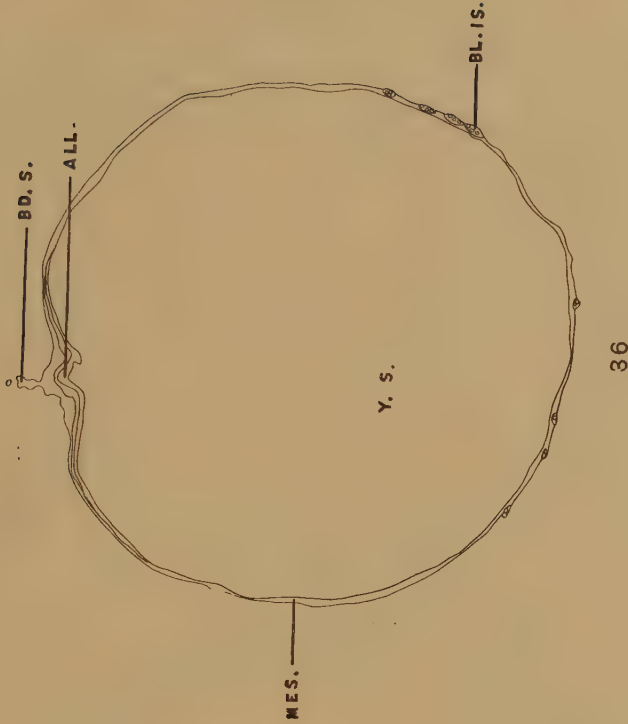


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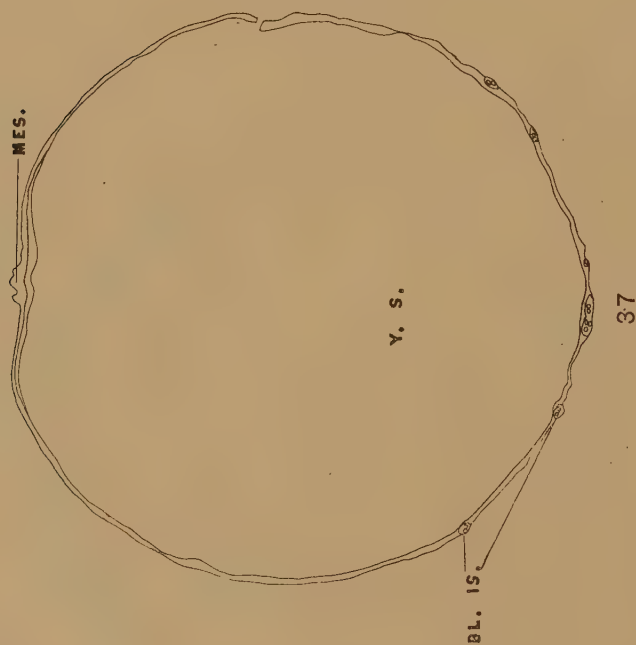
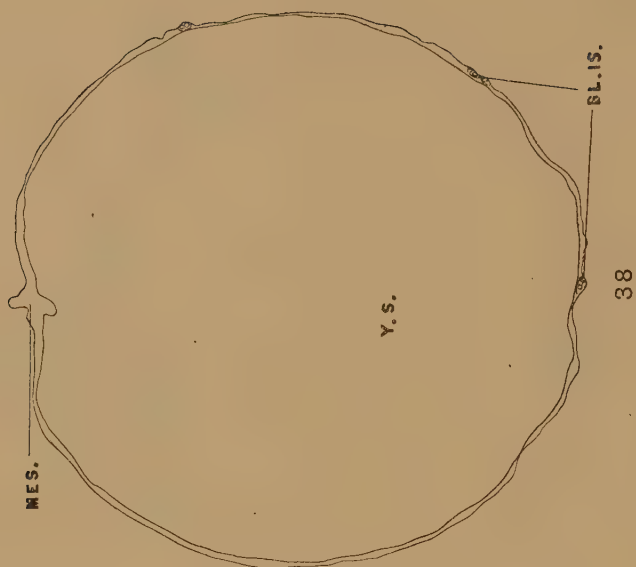


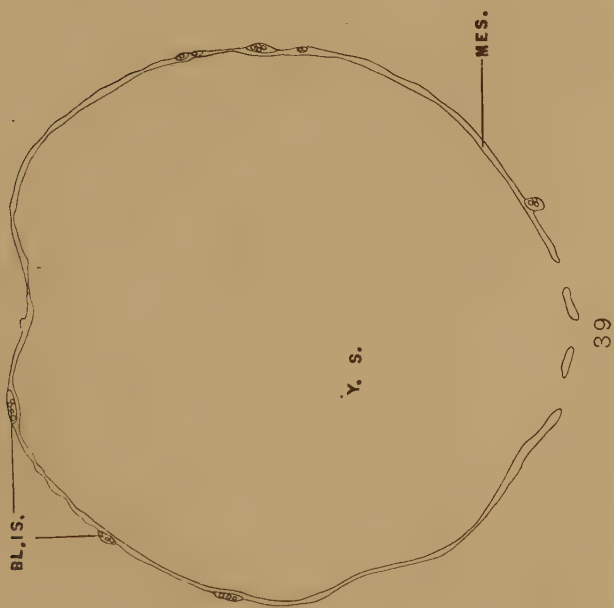


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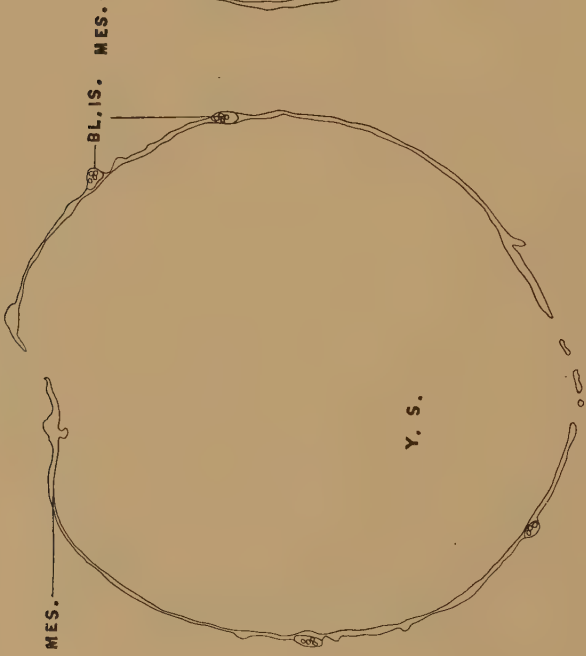
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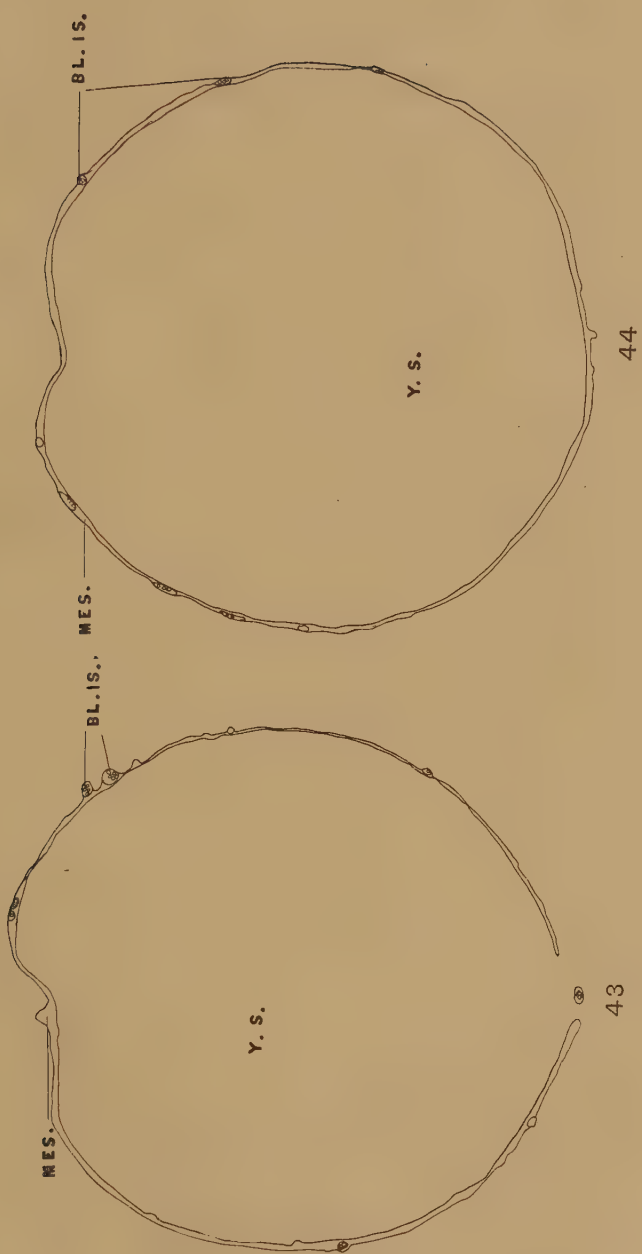


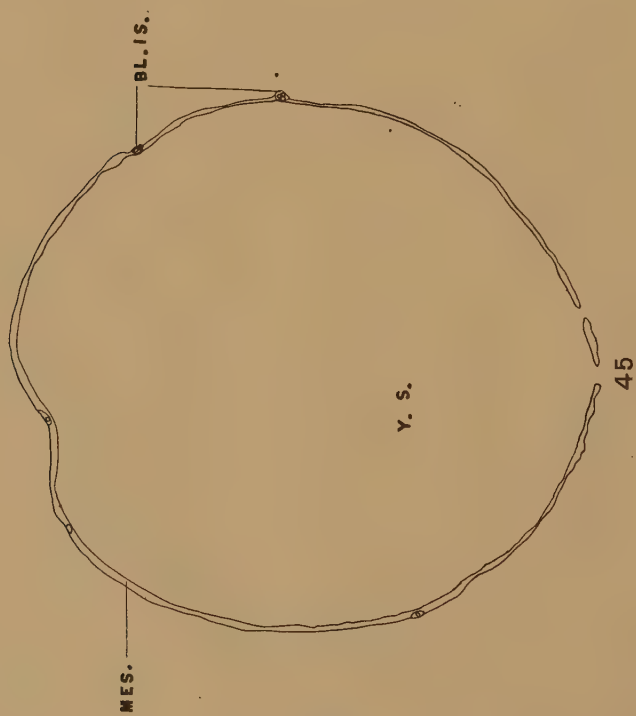
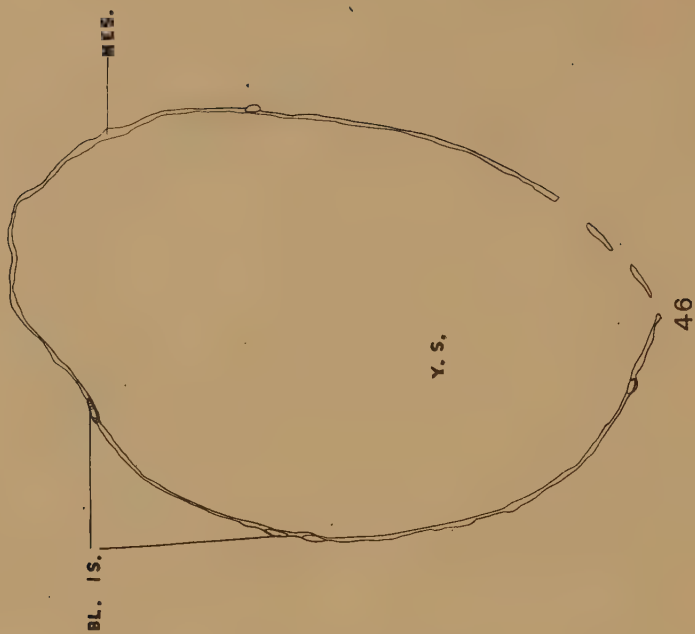


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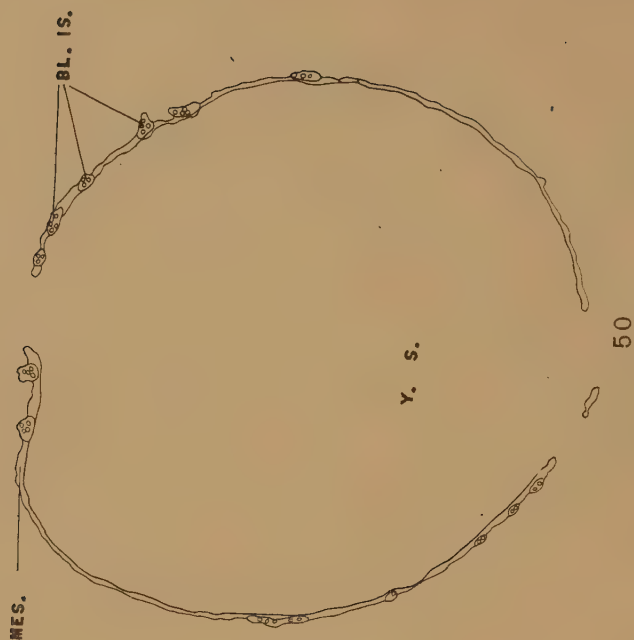


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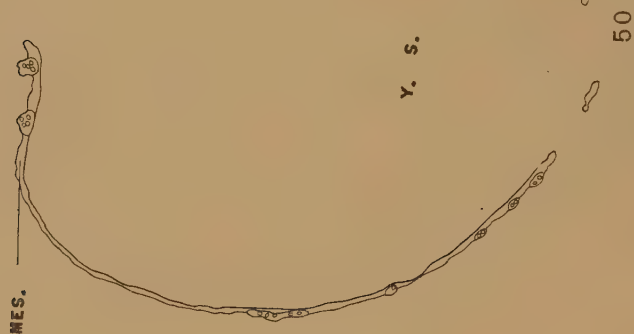




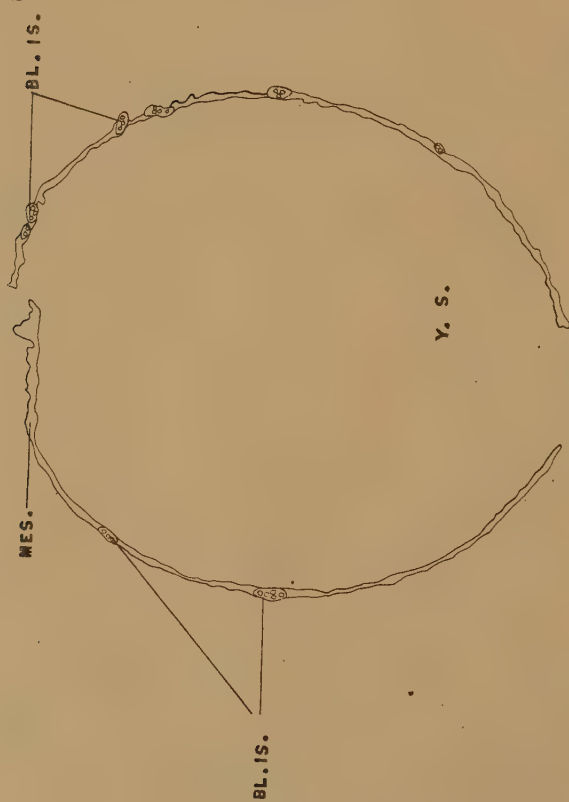




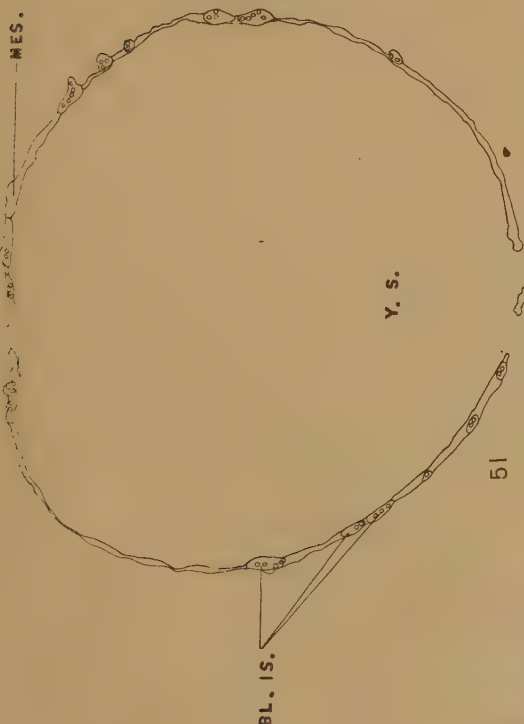
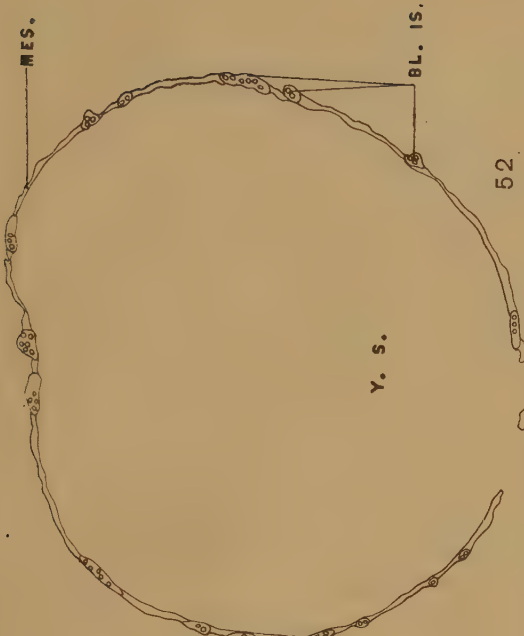
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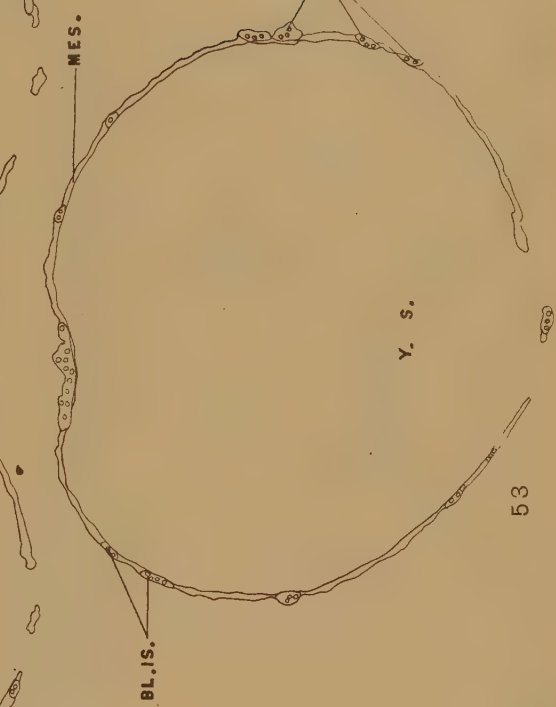


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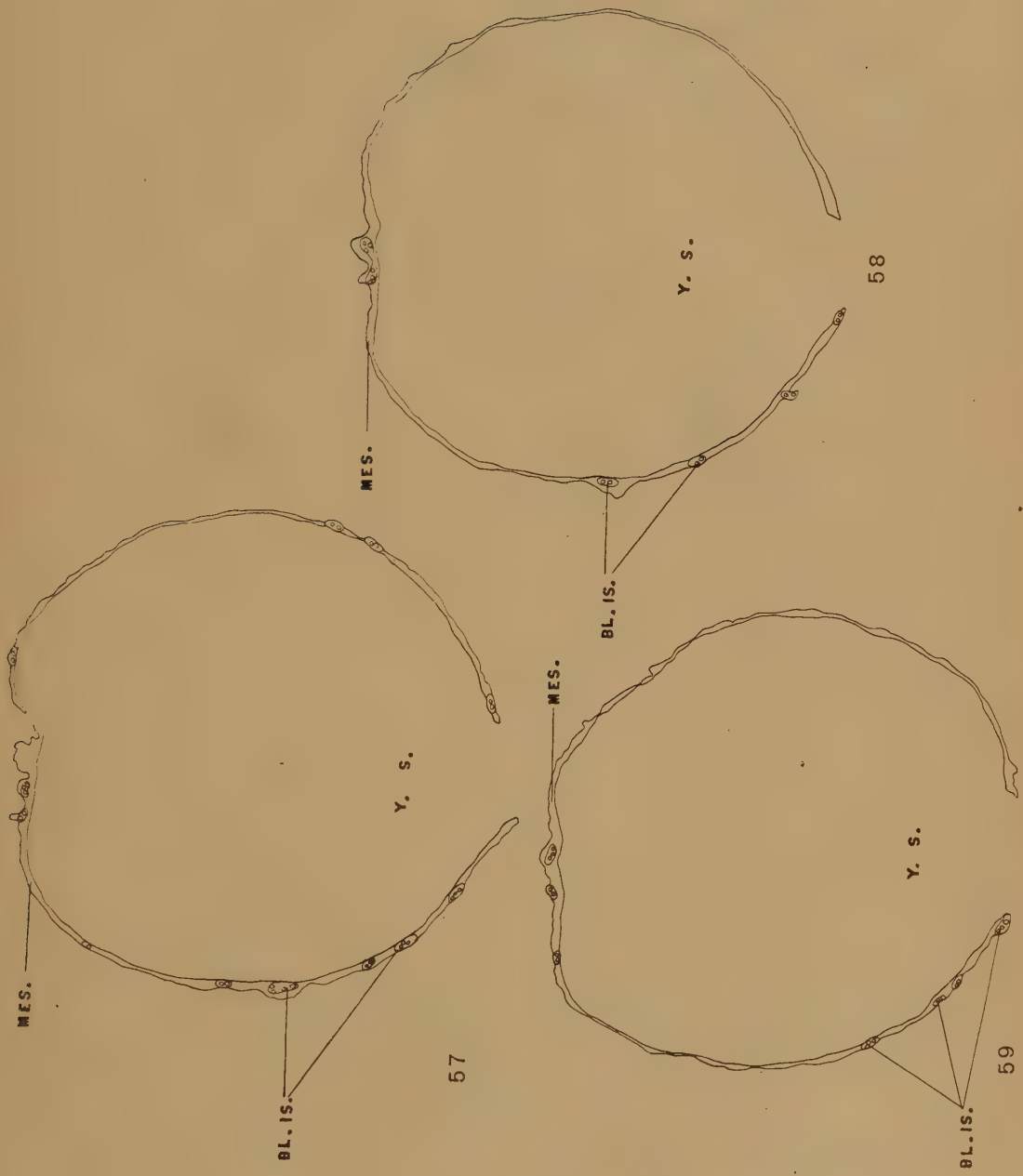


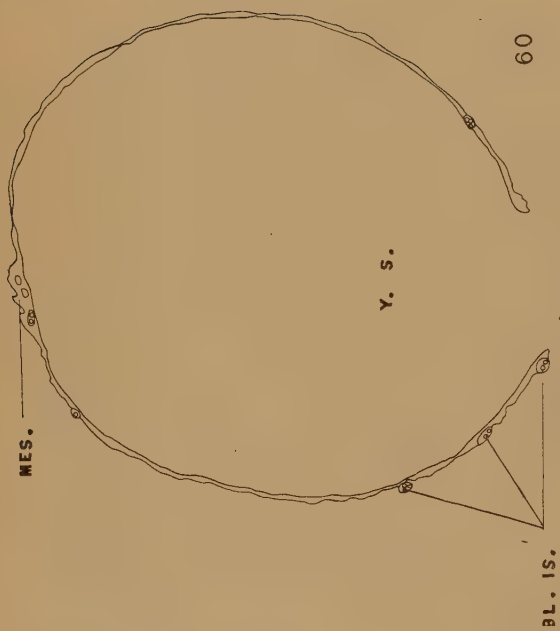
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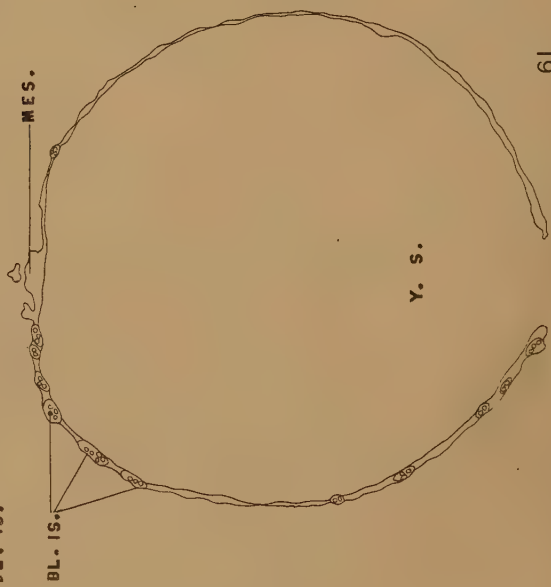
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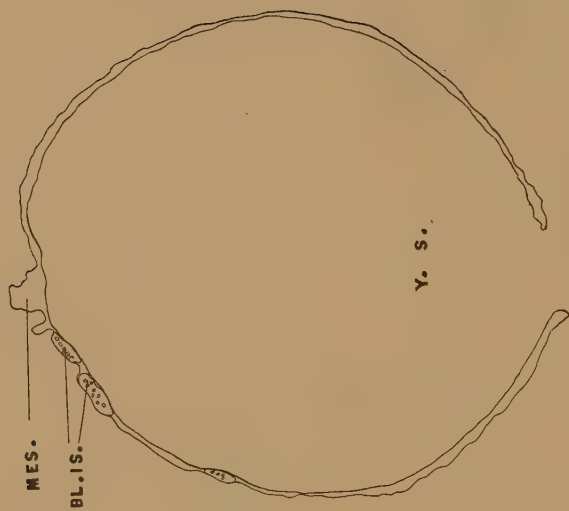




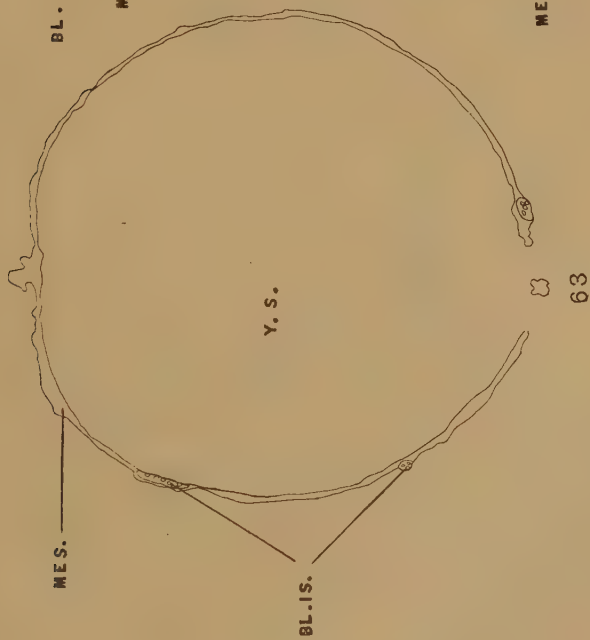
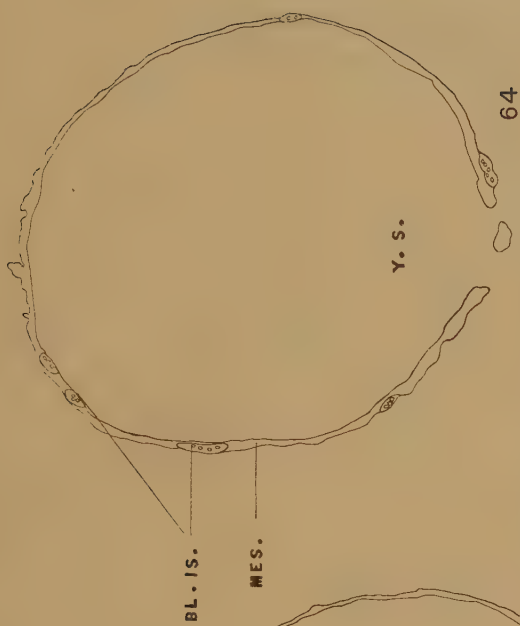
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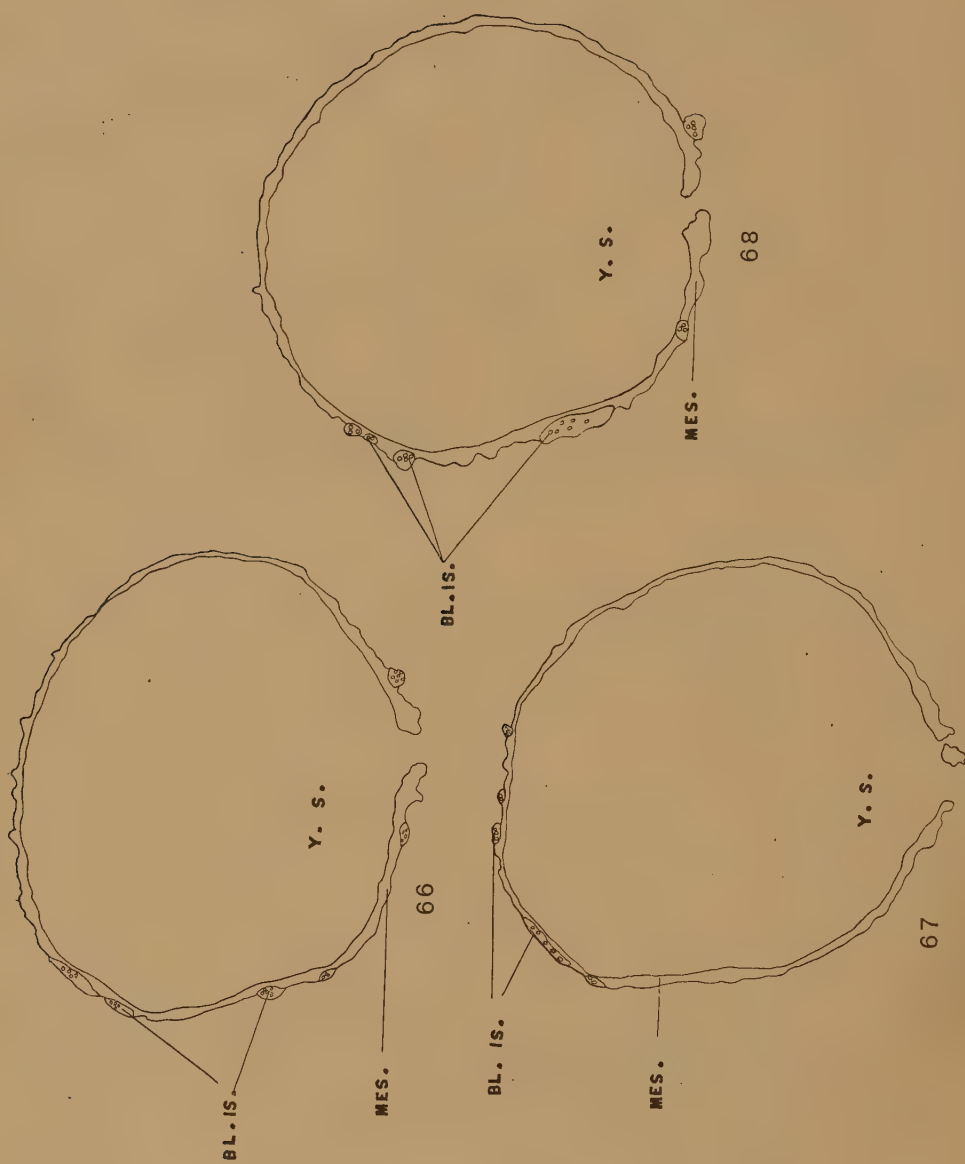


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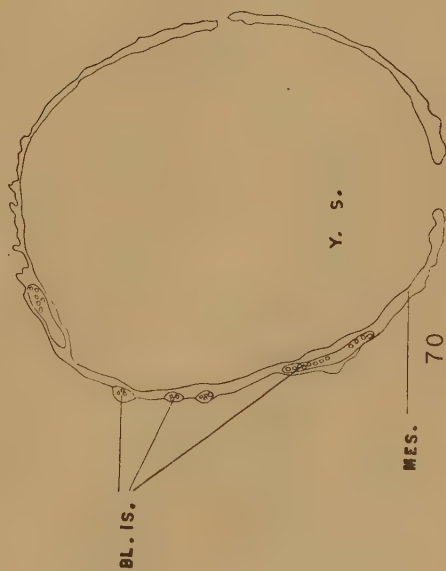
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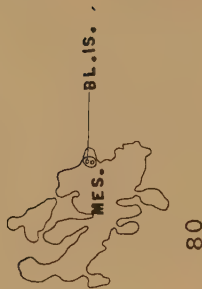
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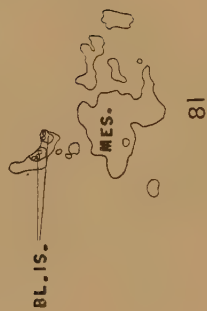
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